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THE VISIBLE STRUCTURE OF THE SECONDARY WALL AND ITS SIGNIFICANCE IN PHYSICAL AND CHEMICAL INVESTIGATIONS OF TRACHEARY CELLS AND FIBERS

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With plates 140-149

INTRODUCTION

THE SECONDARY WALL of plant cells has long been known to be a heterogeneous structure. That it is more or less conspicuously striated and laminated was shown by Mirbel, Von Mohl, Valentin, Meyen, Th. Hartig, and other pioneer anatomists who demonstrated, in addition, that it may be resolved by specific chemical and mechanical treatments into lamellae, fibrils, granules, and other visible units of fairly constant form and size. This led, during the second half of the last century, to prolonged discussions concerning the fundamental structure of cell walls in general, and to much speculation regarding the physiological processes involved in their formation.

Although a voluminous literature developed between 1850 and 1900, no consensus of opinion was reached concerning the exact physical and chemical significance of the visible heterogeneity of the secondary wall. Nor is there a general agreement among different groups of investigators at the present time. It is true that the study of anisotropy, of rod double refraction, of various types of dichroism, and of X-ray diagrams has in recent years contributed much toward a clearer understanding of sub-microscopic structures, and regarding the orientation of such structures in the grosser layers of the secondary wall, but it has not afforded as yet an adequate explanation of the finer types of visible heterogeneity.

¹Parts of these investigations were made by the junior author as a National Research Fellow in Botany.

In view of such facts as these, it seemed desirable to the writers to undertake a detailed investigation of the secondary wall in an endeavor (1) to verify and, if possible, to amplify the observations of previous workers; (2) to correlate results obtained by different techniques and by the study of divergent cell types; and (3) to interpret the visible heterogeneity of the secondary wall in terms of its sub-microscopic structure and of its chemical composition.

In an investigation of this character one is faced, at the outset, by a serious difficulty, upon the solution of which success or failure clearly depends. The range of recorded cases in which the details of wall structure are even vaguely visible — without resorting to the use of softening or hardening processes, of macerating or swelling agents, and of other more or less drastic chemical and mechanical treatments — is very limited. Severe treatments are capable of yielding extremely useful and significant data, but are likely to produce distortions and other artifacts, and therefore must be checked by observations on untreated material. In other words, an adequate system of controls — or means of accurately visualizing the normal structure of the secondary wall — is indispensable.

As indicated in the preceding paper of this series (18), it is possible to section dense woods and other hard tissues without resorting to the use of softening processes which might modify their structure and chemical composition. It seemed advisable, accordingly, to make an extensive survey of a wide range of gymnosperms and angiosperms in search of species that afford clearly defined images of cell wall structure in untreated sections. More than 3000 species, representing 160 families and 40 orders, were examined. It was found that the large-celled woods of various tropical dicotyledons provide unusually favorable material for microscopic investigations. These plants are not bizarre or unusual forms; nor are they confined to any restricted group or genus. They are widely distributed and of not uncommon occurrence in such families as the Theaceae, Monimiaceae, Icacinaceae, Rhizophoraceae, Euphorbiaceae, Flacourtiaceae, etc. When thin (5–10 μ), smoothly-cut sections of the wood are examined in liquids of the right index of refraction, using the best modern optical equipment, the relatively broad expanse of wall in the fiber-tracheids and libriform fibers of certain of these plants reveals finely laminated, striated, and reticulated structures in exquisite detail. By using untreated sections of such plants as controls, it is possible to determine the exact effects upon normal structures of varied chemical and mechanical treatments, and thus to extend the scope of investigation to cover a wide range of less favorable species and tissues.

The following discussion of tracheary cells and fibers is divided into two parts. The grosser and more conspicuous types of layering of the secondary wall are dealt with in Part I; structures which more nearly approach the limits of microscopic visibility, in Part II. As previously stated, considerable is known¹ concerning the physical factors involved in the differentiation of the former structures, which must be clearly visualized and accurately correlated before proceeding to a detailed consideration of the finer types of visible heterogeneity.

TERMINOLOGY

The terms *middle lamella*, *primary wall*, *secondary wall*, and *tertiary wall* have been employed in several fundamentally different senses and to designate entirely different structures. This has led to much confusion in the literature and to serious discrepancies, not only in descriptive morphological work, but also in physiological, biophysical, and biochemical investigations. As a result of our detailed study of the cambium and its derivatives and of our preliminary investigations of other meristems and their derivatives, we attempted, in a former paper (18), to clarify the situation by suggesting that (1) the term *middle lamella* be used synonymously with intercellular substance in referring to the truly isotropic material which separates the walls of adjoining cells; (2) the term *primary wall* should no longer be applied to the first-formed layer of secondary thickening, but should be reserved for the original wall of the cell which is formed in the meristematic region and is carried over in more or less modified form into the fully differentiated tissues; and (3) the term *secondary wall* be used in referring to the strongly anisotropic layers of secondary thickening which are formed after a cell has attained its final size and shape. The term *tertiary wall* is so variously used and interpreted and so confusing that its use should be discontinued. We propose to employ our revised terminology in this and succeeding papers.

I. THE PRINCIPAL LAYERS OF THE SECONDARY WALL

A. LAYERING DUE TO PHYSICAL FACTORS

The secondary wall of normal tracheids, fiber-tracheids, and libriform fibers commonly consists of three layers of different refractive character; (1) a relatively narrow outer layer, (2) a narrow inner layer, and (3) an intervening layer of variable thickness. When thin, per-

¹For comprehensive reviews of the literature relating to this subject, the reader is referred to Van Iterson (30, 31) and Frey-Wyssling (13).

fectly transverse sections of such cells are examined in polarized light between crossed nicols, *Fig. 3*, the inner and outer layers exhibit strong double refraction and are brilliant — except in positions of extinction — whereas the central layer is dark or noticeably less birefringent. The conditions tend to be reversed in longitudinal sections, *Fig. 2*, in which the central layer shows intense double refraction, and the inner and outer layers are dark or less conspicuously birefringent. In other words, as shown long ago by Dippel (7) and others, the secondary wall consists of anisotropic layers which are dark or brilliant in polarized light depending upon the plane of sectioning of the cell or upon the angle from which the wall is viewed.

Our extensive survey of gymnosperms and angiosperms has demonstrated that most tracheids, fiber-tracheids, and libriform fibers are provided with a secondary wall of this 3-layered type. The narrow inner and outer layers are of relatively constant thickness, not only in different parts of a given plant but also in plants of different systematic affinities. Variations in thickness of the secondary wall are due, therefore, primarily to fluctuations in the width of the central layer. When the secondary wall is thin, as in the tracheids of the early wood of many conifers, the inner and outer layers are so closely approximated that the tenuous intervening central layer is invisible in polarized light, except in very thin ($3-7\ \mu$), perfectly transverse sections of straight-grained tissue. In thicker or obliquely cut sections, the width of the inner and outer layers is much exaggerated by the scattering of light from these intensely birefringent structures. This fogs and conceals the central layer, just as the closely approximated brilliant outer layers of adjacent cells commonly obscure the tenuous primary walls and middle lamella (compare *Figs. 1* and *3*).

Deviations from the normal 3-layered type of secondary wall are of not infrequent occurrence. Thus, many thick-walled libriform fibers and fiber-tracheids have no clearly differentiated inner layer, whereas others have more than three layers of varying width and birefringence, *Fig. 4*. Walls of a multiple-layered, anisotropic type, which are of relatively sporadic occurrence in the fiber-tracheids and libriform fibers of dicotyledons, are characteristic features of the fibers of many monocotyledonous stems. In transverse sections of such fibers, *Fig. 6*, there are narrow brilliant zones in polarized light which alternate regularly with broader and conspicuously less birefringent ones. Variations in the thickness of the secondary wall of these cells are due largely to variations in the number of successively formed layers.

The optical behavior of the anisotropic layers of the secondary wall

of tracheary cells and fibers is closely correlated with the orientation of striations and so-called fibrillar structures, which are visible in cells that have been subjected to various chemical and mechanical treatments. When the striations and fibrils are arranged parallel, or nearly parallel, to the long axis of a tracheary cell or fiber, a layer is dark in sections cut at right angles to this axis, but is brilliant in longitudinal sections and in surface view — except, of course, in the four positions of extinction. The intensity of the birefringence varies in obliquely cut intervening sections, decreasing as the plane of section approaches that of a truly transverse section. On the contrary, where the striations and fibrils are arranged approximately at right angles to the long axis of a cell, a layer is brilliant in cross sections and in surface view, but is dark in thin longitudinal sections, *Fig. 2*, which transect the fibrillar structure. When the striations and fibrils have a helical arrangement and, therefore, are obliquely oriented in relation to the major axis of the cell, a layer is brilliant in surface view and more or less birefringent in both transverse and longitudinal sections. If the helix has a pitch of approximately 45° , an oblique section, which is cut parallel to the striations and fibrils on one side of the cell, will transect these structures on the opposite side of the cell. Thus, in such sections, the layer will exhibit both isotropy and strong double refraction; i.e., it will be dark on one side of the section and brilliant on the opposite side. Changing the fibrillar orientation from a left-handed to a right-handed helix or *vice versa* will not alter the birefringence in transverse or in longitudinal sections so long as the angle of obliquity remains constant.

In the typical 3-layered secondary walls of tracheids, fiber-tracheids, and libriform fibers, the striations and fibrils of the central layer are oriented parallel to the long axis of the cell, or at angles which do not deviate excessively from that axis; whereas those of the inner and outer layers are arranged more nearly at right angles to the major axis of the cell. Thus, the central layer exhibits strong double refraction in longitudinal sections, *Fig. 2*, and isotropy or relatively feeble double refraction in transverse sections, *Figs. 1 and 3*; whereas the conditions are reversed in the case of the inner and outer layers of the secondary wall. In multiple-layered walls of the type illustrated in *Fig. 6*, the orientation alternates regularly from parallelism to the major axis of the cell in the broader layers to marked obliquity in the narrower ones. The former layers exhibit intense double refraction in longitudinal sections; the latter layers, in transverse sections.

In the case of optical anisotropy, the so-called index-ellipsoid has, according to Frey-Wyssling (13), a major axis (N_γ) which is oriented

parallel to the striations and fibrils, and two minor axes (N_α and N_β) which are placed at right angles to these structures. On the contrary, in the case of swelling-anisotropy, the ellipsoid of expansion has two major axes which are oriented at right angles to the striations and fibrils, and a minor axis which is parallel to these structures. Therefore, the dark layers of *Figs. 1, 3, and 6*, which have longitudinal striations, expand laterally, increasing in both width and circumference; whereas the strongly birefringent layers, the striations of which are oriented more nearly at right angles to the long axis of the cell, are unable to do so and expand longitudinally. Where the dark layers are of considerable width, they tend, by their excessive lateral expansion, to disrupt the thin birefringent layers, as indicated in *Fig. 7*.

The strongly anisotropic behavior of the secondary wall suggests that its layers are composed of sub-microscopic units which have definite planes of orientation, and that there is a close correlation between the orientation of these units and of such visible structures as striations and fibrils. It was in fact a consideration of these phenomena which led Nägeli to formulate the Micellar Hypothesis.

More recently, X-ray analyses and other physico-chemical investigations have indicated that native cellulose consists of chains of anhydrous glucose residues which are bound together by secondary valences into a space lattice of definite dimensions. These chains are arranged parallel to each other, and, in the case of the secondary wall of fibers and of *Valonia*, are oriented parallel to the striations and fibrils — as shown by Katz (17) and by Astbury and his co-workers (1). Furthermore, there is much cumulative evidence¹ from detailed investigations of anisotropy, of rod double refraction, of various forms of dichroism, and of X-ray analyses which suggests that the cellulose chains are not uniformly distributed throughout the secondary wall, but are aggregated into more or less vaguely defined anisotropic units the major axis of which is oriented parallel to that of the visible striations and fibrils.

In view of such facts as these, it is evident that layering of the type discussed on preceding pages is not due fundamentally to differences in chemical composition, but rather to changes in the orientation of anisotropic units of cellulose in the successively formed layers of the secondary wall.

B. LAYERING DUE TO CHEMICAL FACTORS

The broad central layers of normal fiber-tracheids and libriform fibers frequently have subsidiary layers of varying width which are much

¹This evidence has recently been summarized and discussed by Frey-Wyssling (13).

intensified by differential staining, *Fig. 8*. These subsidiary layers, unlike those illustrated in *Fig. 4*, are not closely correlated with variations in the orientation of the anisotropic cellulose, but are due to differences in lignification or to variations in the distribution of non-cellulosic constituents. They may be eliminated by delignification and other standard treatments for the purification of cellulose. It should be emphasized in this connection that the anisotropic layers of normal tracheids, fiber-tracheids, and libriform fibers are coherent even in walls that have been treated to remove their non-cellulosic constituents. There are evident planes of weakness but no actual discontinuities in the cellulosic matrix.

Conspicuous discontinuities are, however, of not infrequent occurrence in the peculiar tracheids of "compression wood," in so-called gelatinous fibers, in certain types of bast fibers, and in sclereids. They are due to narrow layers of *truly isotropic* material which contain little, if any, cellulose. Thus, when sections of unlignified or delignified cells are treated with standard solvents of pectic compounds and hemicelluloses, the layers dissolve and liberate the anisotropic layers of cellulose which may be slipped apart as shown in *Fig. 26*. These truly isotropic layers may be accentuated by differential staining and are clearly visible in ordinary light, *Fig. 21*. They present some difficulties, however, when sections are examined in polarized light between crossed nicols. For example, the entire laminated structure in *Fig. 21*, with the exception of the narrow outer layer, is dark in polarized light, owing to the fact that the orientation of cellulose in the anisotropic layers is parallel to the long axis of the cell. Therefore, the truly isotropic layers are concealed in transverse sections, but they are clearly visible in radial longitudinal sections and appear as dark lines between the birefringent layers of cellulose. There are similar tenuous isotropic films in the fibers of *Pandanus* on the outside of each narrow anisotropic layer, *Fig. 6*. They are masked in both transverse and longitudinal sections, since the broader anisotropic layers of cellulose are dark in cross sections, and the narrower ones are dark in longitudinal sections.

C. LAYERING IN SCLEREIDS AND NON-FIBROUS SCLERENCHYMA

It should be noted, before passing to a detailed consideration of the finer types of visible structures, that sclereids and other types of non-fibrous sclerenchyma have a fundamentally different type of secondary wall. The anisotropic layers of such cells—at least in tissues of the higher plants that we have examined thus far—show no conspicuous striations or fibrillar structures, either in the untreated or in the swollen

condition of the cell wall. Furthermore, the anisotropic layers are brilliant in polarized light in all planes of section of the secondary wall, but are dark in surface view. The birefringent layers alternate more or less regularly with others which are dark in all planes of view, *Fig. 5*. A detailed discussion of these cells and of other non-fibrous types is reserved for subsequent papers of this series.

II. THE FINER VISIBLE STRUCTURES OF THE SECONDARY WALL

A. NORMAL 3-LAYERED TRACHEIDS, FIBER-TRACHEIDS, AND LIBRIFORM FIBERS

As stated in Part I, variations in thickness of the secondary wall of normal tracheids, fiber-tracheids, and libriform fibers are due primarily to fluctuations in the width of the central layer, which may attain a radial breadth of more than $15\ \mu$ in the large-celled woods of various tropical dicotyledons. Therefore, the central layer provides more favorable material for sectioning and for study at high magnifications than either the inner or the outer layers which are so tenuous as to present serious optical difficulties.

Figure 10 is a transverse section of the wood of *Siparuna bifida* (P. & E.) A. DC. cut without preliminary softening or other modifying treatments. The broad central layer of the secondary wall is strikingly heterogeneous and exhibits a complex pattern of anastomosing radial striations. The striations are clearly visible in unstained sections mounted in water and in other liquids of varying indexes of refraction; and, in white light, are optically of two types, i.e., light and dark. There are corresponding light and dark striations in tangential longitudinal sections, *Fig. 13*. It is evident, accordingly, that the central layer of the secondary wall in these cells is composed of thin plates or lamellae which have a radio-longitudinal or radio-helical orientation. The lighter lamellae are strongly birefringent in polarized light, *Fig. 13*, except in positions of extinction and in sections cut at right angles to the longitudinal axis of the lamellae; whereas the alternating lamellae are dark, or at least comparatively isotropic, in all planes of view.¹

The birefringence of the lighter lamellae is not due entirely to rod double refraction, as may be determined by examining sections in a graded series of liquids of varying indexes of refraction. Nor is the

¹Extremely thin, smoothly cut sections are essential for critical examination in polarized light. If the sections are too thick or are scratched or roughened in cutting, the tenuous dark lamellae will be completely masked by the glare of light from the strongly birefringent lamellae.

apparent isotropy of the intervening lamellae due solely to the masking effects of lignification or to the presence of other non-cellulosic constituents. The walls of immature unlignified cells show identical patterns and a similar differentiation into lamellae of two distinct categories of birefringence, as do delignified cells that are treated for the removal of hemicelluloses and other non-cellulosic constituents.

By subjecting untreated sections to the action of such swelling agents as acids, alkalis, chloro-iodide of zinc or cuprammonium hydroxide, and by carefully controlling the reactions, it is possible to expand the central layer and its constituent lamellae without distorting or seriously modifying the original structural pattern (compare *Figs. 10* and *11*). As the central layer expands and enlarges under the microscope, successively finer details of structure become visible. The lamellae are not discrete homogeneous entities, and are resolved during the expansion of the central layer into aggregations of elongated heterogeneous complexes of varying degrees of fineness which grade down to the limits of microscopic visibility. The darker lamellae are compact sheets of relatively isotropic material which contain a low ratio of birefringent complexes. On the contrary, the lighter lamellae are aggregations containing a high ratio of birefringent complexes and a low ratio of apparently isotropic ones. There are no discontinuities in the structural pattern which is firmly knit together by lateral anastomoses and interlocking complexes.

After treatment for the removal of non-cellulosic constituents, the purified cellulose exhibits a similar structural pattern, which upon swelling, *Fig. 14*, is resolved into a complex and firmly coherent matrix, having elongated, intercommunicating interstices of varying degrees of fineness. The darker and more compact parts of the matrix, which correspond to the lighter lamellae of *Fig. 10*, are strongly birefringent in longitudinal sections and show conspicuous dichroism when carefully stained with congo red or chloro-iodide of zinc; whereas the lighter and more porous parts of the matrix, which correspond to the darker lamellae of *Fig. 10*, are so feebly birefringent that they appear to be comparatively isotropic.

Conversely, when the central layer is freed of cellulose by treatments with 72% sulphuric acid, the details of the swollen pattern are preserved in the so-called "lignin" residue, *Fig. 11*, which also is a complex and firmly coherent structure, having elongated, intercommunicating interstices of varying degrees of fineness. The lighter, finer residues of the originally birefringent lamellae exhibit well defined rod double refraction in longitudinal sections; whereas the darker, denser residues of the originally isotropic lamellae do not.

It is evident from a detailed comparison of *Figs. 11* and *14*, that the denser parts of the "lignin" residue correspond to the more porous parts of the matrix of purified cellulose, and that the "lignin" residue may be interpolated within the interstices of the swollen cellulose. Furthermore, the rod double refraction of the lighter lamellae of the "lignin" residue suggests that the two interpenetrating complexes grade downward in size far below the limits of microscopic visibility. In other words, each of the visible parts of the original structural pattern is heterogeneous and composed of optically different complexes. Removal of either the "lignin" or the cellulose leaves a coherent matrix of varying texture and porosity.

It is possible to reconstruct the structural pattern of the swollen cellulose from the "lignin" residue or *vice versa*, since they are positive and negative images of the same pattern. Although swollen sections of purified cellulose afford excellent preparations for visual examination, they are difficult objects for photographic reproduction. Therefore, a majority of our photomicrographs were made from "lignin" residues.

The structural pattern of the central layer is not a constant; it varies greatly not only in different groups of plants, but also at times in homologous cells of the same plant, and even within the wall of a single cell. For example, in *Siparuna bifida*, the two optically different complexes may be segregated into coarsely radial patterns which are clearly visible in untreated sections, *Fig. 10*, or they may be diffused in finer radio-reticulate patterns, *Fig. 16*, the finest of which are invisible in unswollen sections of the secondary wall. In such cells, conspicuous concentricities usually are due either to abrupt changes in the texture of the structural pattern, *Fig. 11*, or to zones of varying intensities of lignification, *Fig. 9*. The former persist in purified cellulose; the latter are eliminated during delignification.

Structural patterns of a basically concentric type are, however, of common occurrence in the normal tracheids of conifers, *Fig. 18*, and in the fiber-tracheids or libriform fibers of such dicotyledons as *Poraqueiba sericea* Tul., *Fig. 15*. In the central layer of these cells, the optically different complexes are segregated into concentric lamellae of varying widths and spatial groupings. The lamellae are of two types, i.e., strongly birefringent and comparatively isotropic. They are not discrete homogeneous entities, but may be resolved by treatment with swelling agents into complexes of varying degrees of fineness. As in the case of *Siparuna bifida*, the darker lamellae are compact aggregates of relatively isotropic material, *Figs. 15* and *18*, and contain a low ratio of birefringent cellulose; whereas the alternating lighter lamellae are composed largely of birefringent cellulose and contain a low ratio of

isotropic material. The structural pattern persists in delignified sections which are treated with standard solvents of hemicelluloses and of other non-cellulosic constituents. When the purified cellulose is swollen, it appears as a complex and firmly coherent matrix, which exhibits a structural differentiation into compact, strongly birefringent and looser, comparatively isotropic lamellae.

It should be emphasized, in this connection, that the concentric structure of swollen cotton hairs — to which the work of Balls (2) has directed so much attention — appears to be due fundamentally to a similar structural pattern. When extremely thin, very smoothly cut sections of raw or purified cotton are treated with diluted Schweizer's reagent and are examined in polarized light between crossed nicols, the lamellae are, during the early stages of swelling, clearly of two optically different types, i.e., strongly birefringent and comparatively isotropic. During subsequent swelling, *Fig. 17*, the central layer is resolved into a complex and firmly coherent, spongy structure, the conspicuously birefringent parts of which are denser and obviously contain a higher ratio of cellulose than the more porous, intervening parts. In other words, the structural patterns of the central layers of cotton hairs, *Fig. 17*, of coniferous tracheids, *Fig. 18*, and of the fiber-tracheids of *Poraqueiba sericea*, *Fig. 15*, appear to be of a fundamentally similar type. In cotton hairs, as in tracheary cells, the width of the concentric lamellae is not a constant, but varies within relatively wide limits.

The structural pattern of cotton can not be due to a segregation of cellulosic and non-cellulosic constituents, since the central layer of cotton is composed of practically pure cellulose — the low ratio of non-cellulosic constituents in cotton is confined chiefly to the so-called cuticle or primary wall and to the lumen of the cell. Nor can the concentricities be due merely to inequalities in the penetration or modifying effects of the swelling agent, as may be demonstrated by cross-correlating the structural patterns of different hairs from the same boll. For example, in *Fig. 17*, in passing outward from the lumen, there is the following sequence of lamellae: six narrow alternating light and dark zones, an unusually wide light zone, two broad dark zones separated by a narrower light zone, two narrow dark zones and three narrow light zones, and six broad dark zones separated by narrower light zones. The fact that this identical complex of varying concentricities occurs in other hairs from the same boll can not be due to purely fortuitous circumstances, but might be due, either directly or indirectly, to the modifying effects of environmental factors upon the developing hairs.

Nor can the structural patterns of tracheids, fiber-tracheids, and libri-

form fibers be due to inequalities in the penetration and modifying effects of the swelling agents, since the patterns are visible under favorable conditions in untreated sections. Thus, the striking similarities in the finer visible structures of the central layer of unligified and deligified cells and of "lignin" residues indicate that there are fundamental structural differences in the underlying cellulose to which the pattern of lignification must more or less closely conform.

Combinations of radial and concentric patterns of varying texture and complexity are of common occurrence in the fiber-tracheids and libriform fibers of dicotyledons.¹ In such cells there may be abrupt transitions within the central layer from coarse to fine texture and from radio-reticulate to concentric arrangements and *vice versa*. *Fig. 19* is a transverse section of the wood of *Tetramerista glabra* Miq., cut without preliminary softening or other drastic treatments. It illustrates a type of complex radio-concentric structure which is clearly visible in unstained sections mounted in water and other liquids of varying indexes of refraction. The pattern is complicated, however, as is so often the case in cells of this type, by the presence of zones of varying intensities of lignification. A radio-concentric pattern of much finer texture is illustrated in *Fig. 20*.

In the case of the more heavily lignified zones of such central layers, *Figs. 9 and 20*, both the birefringent and the comparatively isotropic parts of the structural pattern persist in "lignin" residues; whereas, in the less intensely lignified zones, the birefringent parts leave no structural residue. It is of interest, in view of the significance that has been attached to the work of Freudenberg and his co-workers (12), that in longitudinal sections the residues of heavily lignified parts exhibit conspicuous rod double refraction; whereas the residues of the less intensely lignified parts do not.² In other words, there appear to be submicroscopic structural differences in the two optically different complexes of the structural pattern which are reflected in their "lignin" residues. Furthermore, as previously noted, when delignified sections are stained with chloro-iodide of zinc or congo red, the strongly birefringent parts of the structural pattern may become markedly dichroic; whereas the more nearly isotropic parts do not.

The observational and experimental data that we have assembled in

¹Concentric patterns with tenuous radial groupings are of not infrequent occurrence in the tracheids of conifers.

²Rod double refraction is visible only in the parts of the lignin residue which are strongly birefringent in the original material. Therefore, it can not be seen in sections which transect the so-called fibrillar structure, since all the cellulose is dark in polarized light in such planes of section.

our extensive survey of a wide range of gymnosperms and angiosperms indicate that the central layer of normal tracheids, fiber-tracheids, and libriform fibers is composed, in all cases, of a complex and firmly coherent matrix of cellulose with elongated, intercommunicating interstices. Within these interstices more or less "lignin" and other non-cellulosic constituents may be deposited. The denser and more porous parts of the cellulosic matrix exhibit striking contrasts in birefringence, which are accentuated by lignification. Where these optically different parts are diffused in various patterns of fine texture — as is usually the case in the tracheids of conifers and in the fiber-tracheids and libriform fibers of many dicotyledons — the structural complexes are invisible in untreated sections of the secondary wall, but may be swollen to microscopically visible dimensions, *Figs. 9, 12, 15, 16, 18, and 20*. On the contrary, where the two optically different parts are segregated into coarser structural complexities, *Figs. 10, 13, and 19*, the patterns are clearly visible in unswollen sections.

The cellulosic matrix of the central layer is composed, in all cases, of anastomosing elongated complexes which are oriented parallel to the long axis of the cell or in a helical arrangement. In fact, it is these elongated complexes of two optically different types, *Fig. 13*, which give a longitudinally or helically striated appearance to the central layer and determine its helical or longitudinal planes of cleavage into so-called fibrils. In other words, fibrils are heterogeneous shredded parts of an originally continuous and coherent matrix.

Although there are serious optical difficulties in studying the tenuous inner and outer layers of the secondary wall in sectional view, the striated appearance of these layers in surface view strongly suggests that they have similar structural patterns, the elongated, strongly birefringent complexes of which are oriented more nearly at right angles to the longitudinal axis of the cell.

B. MULTIPLE-LAYERED FIBERS

The orientation of the elongated complexes of the structural pattern may be relatively uniform throughout the central layer of tracheids, fiber-tracheids, and libriform fibers, or it may deviate more or less in successively formed parts of this layer. Not infrequently, the changes in orientation are correlated with fluctuations in the texture of the structural pattern. Where the deviations are of considerable magnitude, they may be detected in polarized light, as illustrated in *Fig. 4*. The brilliant internal zones resemble the inner and outer layers of the secondary wall in having their birefringent complexes oriented more

nearly at right angles to the longer axis of the cell, and therefore are bright in transverse sections.

Although there is a superficial similarity between *Fig. 4* and *Fig. 6*, the two cell walls are of a fundamentally different type. In the fibers of *Pandanus*, *Fig. 6*, as in the libriform fibers of various representatives of the Flacourtiaceae, *Figs. 21* and *26*, and in the bast fibers of ramie and of other dicotyledons, there are, as previously stated, actual discontinuities in the cellulosic matrix produced by narrow isotropic films of a non-cellulosic character. It should be emphasized, in this connection, however, that the individual anisotropic zones of these multiple-layered fibers have complex structural patterns of the general types discussed on preceding pages. For example, *Fig. 21* is a transverse section of the unswollen wall of *Homalium luzoniense* F. Villar. The layers of cellulose have a radio-reticulate pattern, the finer structural details of which are more clearly visible in swollen sections or in "lignin" residues, *Fig. 22*. The elongated birefringent complexes of the structural pattern are oriented parallel to the long axis of the cell. Therefore the entire complex of layers is dark in polarized light in transverse sections. Coarsely radial patterns of the type illustrated in *Fig. 10* are of not uncommon occurrence in the individual anisotropic layers of certain bast fibers; whereas in *Pandanus*, *Fig. 7*, the two optically different aggregates of cellulose are diffused in a pattern of unusually fine texture. Where the strongly birefringent complexes are oriented closely parallel to the longitudinal axis of the cell, the layer is dark in cross sections, *Fig. 6*, and merges with the truly isotropic film of non-cellulosic material; where they are oriented more nearly at right angles to the major axis of the cell, the layer is brilliant in transverse sections.

Variations in the orientation of cellulose in successively formed parts of the secondary wall have a marked effect upon the swelling of tracheary cells and fibers. Owing to its specific anisotropy, the cellulose expands at right angles to the so-called fibrillar axis, and, during extensive lateral swelling produced by strong chemical reagents, actually contracts in a direction parallel to this axis. In the case of isolated, delignified tracheary cells and fibers having normal 3-layered secondary walls, the laterally expanding central layer frequently splits the tenuous, longitudinally expanding outer layer into a series of constricting rings and helical bands, *Fig. 23*, and bulges outward between these structures. This ring-bead type of swelling occurs in cotton and has received considerable attention in literature dealing with commercial fibers. Although the so-called cuticle or primary wall may aid at times in bead formation, the controlling factor in cotton hairs, as in tracheary cells

and fibers, appears to be differences in orientation of cellulose in the outer and central layers of the secondary wall. There are no transverse plates of non-cellulosic material in the secondary wall which are concerned in ring-bead formation as hypothesized by Lüdtke (21).

In the case of multiple-layered tracheary cells and fibers, it is possible to verify conclusions based upon the study of cells of the 3-layered type. We have shown that the concentric anisotropic layers of various representatives of the Flacourtiaceae, *Figs. 21, 22, and 26*, are separated by films of non-cellulosic material, and that the orientation of the cellulose is constant except in the outermost layer of the secondary wall, where it is more nearly at right angles to the longitudinal axis of the cell. When such cells are partly or completely delignified and are swollen in cuprammonium hydroxide, the internal complex of anisotropic layers expands laterally and disrupts the tenuous outer layer into constricting rings, *Fig. 27*, or helical bands, *Fig. 24*. The internal layers of cellulose — which may be slipped apart as shown in *Fig. 26* — expand more or less in unison, *Figs. 24 and 27*, and no subsidiary internal constrictions are formed.

On the contrary, in the multiple-layered fibers of *Pandanus* and of other monocotyledons — which have similar isotropic films of non-cellulosic material, but where the orientation of the cellulose changes in the successively formed anisotropic lamellae — each of the narrow anisotropic layers, *Fig. 6*, may be disrupted by the lateral expansion of the broader layers, *Fig. 7*, and in the case of entire, delignified fibers, may give rise to constricting rings and helical bands, *Fig. 25*. In other words, the fiber behaves as if it were composed of several two-layered secondary walls, each of which swells in turn, forming similar ringed and beaded structures, *Fig. 25*. The two outermost layers swell first, the expansion working from the ends towards the center of the cell. The first formed ringlike constrictions commonly determine the position of subsequently formed internal constrictions.

Multiple-layered fibers of the *Pandanus* type are of common occurrence in the primary tissues of the stems of many monocotyledons. It is evident from Lüdtke's (20, 22) figures and descriptions that the fibers of bamboo are of this structural type, and that they exhibit similar phenomena during their expansion in such swelling agents as cuprammonium hydroxide. It is obvious, in addition, that purely physical phenomena of swelling have been misinterpreted by Lüdtke as evidence for the existence of transverse plates (*Querelemente*) of non-cellulosic material.

DISCUSSION

A. CONCENTRICITIES

The secondary walls of tracheary cells and fibers are extremely complex and variable structures. Therefore, it is misleading and fruitless to attempt to homologize all types of fibers in a single structural model. For example, there are five different types of visible concentricities, due to:

1. The segregation of two optically different aggregates of cellulose into concentric patterns.
2. Abrupt changes in the form or texture of the structural pattern.
3. Changes in the orientation of the elongated birefringent complexes of the structural pattern.
4. Varying intensities of lignification or differences in the distribution of non-cellulosic constituents within the structural pattern.
5. Alternation of cellulosic and non-cellulosic layers.

In so far as we are able to judge from a study of a wide range of gymnosperms and angiosperms, most, if not all, tracheary cells and fibers exhibit more or less conspicuous concentricities of the third type, i.e., those due to changes in the orientation of the elongated birefringent complexes of the structural pattern, but the number and magnitude of the deviations in orientation are variable. Inability to detect such concentricities appears to be due to inadequate techniques or to errors of interpretation. In most cases, the third type of layering occurs in association with one or more of the other four types of concentricities. Thus, in the secondary wall of cotton hairs, it occurs with the first type; in the fiber-tracheids of *Siparuna bifida*, with the second and fourth types; in the fiber-tracheids of *Tetramerista glabra*, with the first, second, and fourth types; in the fibers of *Pandanus*, with the first and fifth types, etc.

Variations in the intensity of lignification or in the distribution of other non-cellulosic constituents may at times be closely correlated with changes in the orientation or the texture of the structural pattern. For example, the narrow inner and outer layers of the secondary wall may be more heavily lignified than the central layer or *vice versa*. Similarly, the coarser parts of the structural pattern of the central layer may be more heavily lignified or contain a higher ratio of hemicelluloses than the finer parts or *vice versa*. It is such fortuitous correlations as these which have led, in certain cases, to the unwarrantable conclusion that all types of visible heterogeneities in the secondary wall are due primarily to differences in chemical composition.

There are investigators who believe that all fibers are composed of concentric lamellae of cellulose which are held together by non-cellulosic

material. Thus, Lüdtke (21, 22), who has attempted to homologize all types of fibrous cells in a single structural model, is of the opinion that the lamellae are separated by a "Fremdschubstanz" which differs from both cellulose and lignin in its chemical composition. Ritter (26) argues that it is possible to dissect the secondary wall by chemical means into concentric lamellae which may be slipped apart as shown in *Fig. 26*. Lüdtke's conclusions appear to have been derived largely from a study of bamboo fibers; and Ritter's, from investigations of the libriform fibers of elm. We have shown that the anisotropic lamellae of monocotyledonous fibers frequently are separated by films of non-cellulosic material. The libriform fibers of elm are commonly of the so-called gelatinous type, which also are characterized in many cases by having both cellulosic and non-cellulosic lamellae. In such fibers, where there are actual discontinuities in the structural pattern of cellulose, the anisotropic lamellae may readily be separated by chemical treatments and slipped apart. On the contrary, in cotton hairs and in normal tracheids, fiber-tracheids, and libriform fibers, the entire matrix of cellulose is firmly coherent, and can be dissected only by forcibly tearing or rupturing the structural pattern. In *Siparuna bifida* the more obvious planes of weakness in the cellulosic matrix are radio-longitudinal or radio-helical; whereas in cotton hairs or in *Poraqueiba sericea* they are concentric-longitudinal.

B. "FIBRILS" AND OTHER "UNITS" OF CELLULOSE

Since the pioneer days of Von Mohl, Valentin, and Th. Hartig, a succession of investigators have visualized the secondary wall as composed of visible units of cellulose — elementary fibrils, dermatosomes, etc. — that are held together by non-cellulosic material. It is essential to understand the relationship between these units and the visible structural patterns produced by different optical aggregates of cellulose.

We have shown in Part I of this paper that the orientation of the cellulose is correlated with that of the so-called fibrillar structure, as has been demonstrated by analyses of X-ray diagrams, of anisotropy, of dichroism, and of other physical properties of the cell wall. However, these physical correlations are concerned only with the orientation of the fibrillar structure and afford no conclusive evidence that fibrils obtained by chemical or mechanical treatments are discrete entities of constant length or cross sectional area.

Ritter (27) has discussed the length of the so-called fibril and concludes that it is variable. He states that "although fibril segments of only 230 microns in length have been isolated, it seems that some may

be as long or longer than the fiber." Lüdtke (22), on the contrary, claims that the length of fibrils is determined by the presence and spacing of transverse plates of non-cellulosic material. Jancke, working with R. O. Herzog (15), measured the width of fibrils and obtained values of some $0.3\text{--}0.5\ \mu$. Balls and Hancock (3), proceeding upon the assumption that lamellae¹ are composed of a single concentric row of fibrils, inferred that the width of both lamellae and fibrils in cotton is $0.4\ \mu$. Frey-Wyssling (13) tabulates the dimensions of fibrils as $0.4 \times 0.4 \times 100\ \mu$.

Fibrils may be dissected by relatively drastic treatments with oxidizing agents or acids into short segments which are variously designated as dermatosomes, spherical units, ellipsoid bodies, etc. According to Frey-Wyssling (13), dermatosomes have dimensions of $0.4 \times 0.4 \times 0.5\ \mu$; whereas Farr and Sisson (11) state that ellipsoid bodies prepared from cotton have axes of $1.1\ \mu$ and $1.5\ \mu$. Lüdtke (20) believes that dermatosomes are held together by his "Fremdschubstanz"; whereas Farr and Eckerson (9) maintain that the ellipsoid bodies of cotton are jacketed by a pectic cement.

We have demonstrated in Part II that the central layer of tracheary cells and fibers is composed of an extremely complex and firmly coherent matrix of cellulose and that the details of the structural patterns of this matrix grade down to the limits of microscopic visibility. There is no evidence, either in untreated or in carefully swollen fibers, of discrete entities of cellulose, i.e., of fibrils or dermatosomes, which may be liberated simply by dissolving non-cellulosic constituents. The matrix of cellulose is shredded and disrupted during the production of fibrils and dermatosomes, which are heterogeneous fragments of larger size than the finer visible complexes of the structural pattern. In cotton, *Fig. 17*, as in *Pinus*, *Fig. 18*, *Poraqueiba*, *Fig. 15*, and *Siparuna*, *Figs. 10* and *14*, the lamellae obviously are not composed of a single row of adherent fibrils, but are alternating layers of varying width, porosity, and birefringence. The finer, visible, elongated complexes of the lamellae are $0.1\ \mu$ or less in thickness. As indicated at (a) in *Fig. 17*, the cross sectional area of an ellipsoid body of the size postulated by Farr and Sisson covers more than four lamellae and a relatively large number of the finer visible complexes.

The form and size of the fragments which may be dissected from the secondary wall are clearly dependent upon the structural pattern of the matrix of cellulose, and upon the type and severity of the chemical and

¹Balls did not recognize two distinct categories of lamellae and evidently obtained the value of $0.4\ \mu$ by dividing the total width of the wall by the number of denser, strongly birefringent lamellae.

mechanical treatments to which the material is subjected. Splits or cracks develop in the more porous and weaker parts of the matrix, thus liberating the denser parts which contain a higher ratio of birefringent cellulose. In addition, there are submicroscopic, transverse, or oblique planes of cleavage, i.e., "slip planes," to which the work of Von Höhnelt (16) and of Schwendener (29) has directed so much attention. It is these slip planes, rather than Lüdtké's hypothetical "Querelemente," which facilitate the dissection of the fiber and of the elongated complexes of its structural pattern into shorter segments.

It is of interest, in this connection, that a fibrillar structure is visible after the action of 72% sulphuric acid upon longitudinal sections of fibers which yield coherent "lignin" residues. By the use of mechanical pressure during the initial stages of the action of the acid, the walls of tracheary cells, *Fig. 12*, and fibers may be resolved into long "lignin" threads, similar to fibrils. These shreds of the originally coherent framework of "lignin" may be dissected by more drastic chemical and mechanical treatments into nearly isodiametric fragments resembling dermatosomes. As previously stated, the amorphous non-cellulosic constituents are deposited within the elongated, intercommunicating interstices of the cellulose matrix, resulting in two continuous, interpenetrating systems. Neither system is composed of discrete entities of visible dimensions, but each may be disrupted into fragments of varying size and form. If there are actual discontinuities in the systems, they must occur in the submicroscopic field, e.g., in the realm of micelles or of molecular chains. It should be emphasized, in addition, that so-called fibrillar structures are not visible in the secondary walls of parenchyma, of sclereids, or of other cells which exhibit statistical isotropy in surface view. The structural pattern of the cellulose matrix in such walls is of a fundamentally different type from that which occurs in fibrous cells.

Dermatosomes, spherical units, and ellipsoidal particles are difficult to homologize, either as regards their size or their form. They are obtained by the action of oxidizing agents or of acids which tend to modify the cellulose. Neale (24) has summarized the modifying effects of oxidation and hydrolysis as follows: "The loss of strength and fall in viscosity which accompany the hydrolysis or oxidation of cellulose are quite irreversible, and the general term degradation is applied to these changes. The degradation of cellulose is accompanied by the appearance of chemical properties foreign to the original material. The hydrolysis of the glucoside-oxygen bridge causes the appearance of reducing sugar properties which may be quantitatively, though arbitrarily, expressed as 'copper number' or 'iodine number.' The reducing

sugar properties also arise as a result of oxidation and may be accompanied by the development of acidic properties, so that oxidized cellulose may retain traces of caustic alkali or absorb basic dyes. This latter property has been put on the quantitative basis so essential in the chemistry of cellulose in the form of the methylene blue absorption test."

Thus, it may be seen that the action of acids, which are supposed to dissolve some cementing substance and to liberate integral units of cellulose, may actually result in partial degradation of the cellulose. We have found that the staining of hydrocellulose and oxycellulose with ruthenium red is similar to the methylene blue absorption values as listed by Dorée (8). Ruthenium red behaves, in some respects, as a basic dye, and the staining of ellipsoidal particles, obtained by treating cotton with relatively strong acid (10), may be interpreted as an indication of the degradation of the cellulose rather than as evidence for believing that the particles are coated with a pectic cement. Ruthenium red is not a specific test for pectic compounds, as botanists have frequently assumed. It is removed from dilute aqueous solutions by coagulated protoplasm and other nitrogenous substances, by gums, mucilages, hemicelluloses, oxycelluloses, hydrocelluloses, and certain lipoids, as well as by pectic compounds.

Any hypothesis concerning the visible structure of the secondary wall must account not only for the varying structural patterns of a wide range of cells, but also for well known facts regarding the physical and chemical properties of cellulose. In the case of the hairs of the cotton plant, the constituents which do not yield glucose upon hydrolysis are small in amount, and are confined chiefly to the so-called cuticle or primary wall and to the lumen of the cell. There obviously is not a sufficient volume of cutinlike substances or of pectic compounds in the secondary wall to serve as a cementing substance of the type postulated by Lüdtkke (21) or by Farr and Eckerson (9). Furthermore, when cotton is treated with solvents of such constituents, without degrading the cellulose, the structural pattern is not affected. It persists as a firmly coherent matrix of cellulose.

It is now generally admitted that the cellulose molecule is a long chain of glucose residues bound together by oxygen bridges. Furthermore, there is evidence from X-ray analyses, from anisotropy, dichroism, etc., to indicate that cellulose is built up of submicroscopic, crystal-like aggregates of these chains. The length of the cellulose chain and its arrangement within the crystallite are still subjects of dispute. Thus, it is uncertain whether the chain is shorter or longer than the crystallite or of equivalent length, and whether micelles are discrete and separate entities, or merely parts of a continuous system of overlapping chains.

Estimates of the length of cellulose molecules range from 100–3500 glucose residues. The highest value of 3500 units, i.e., that of Kraemer and Lansing (19), is based upon measurements of viscosity. Such molecules would have a length of approximately $1.8\ \mu$, and would be visible microscopically if they were of sufficient thickness, which they obviously are not. Since the cellulose chains are arranged parallel to the so-called fibrillar orientation, and since there are no visible structures which transect this axis, it is possible to conceive of chains of the length postulated by Kraemer and Lansing arranged in an overlapping manner along the fiber axis.

Our investigations indicate that the cellulosic matrix of the secondary wall is composed of complexes of cellulose of varying birefringence which grade down to the limits of microscopic visibility, and that the fundamental units of cellulose are of submicroscopic dimensions. In the case of cotton, the available chemical and physical data make it appear improbable that the variations in birefringence are due to differences in chemical composition. Correns (5) recognized, more than 40 years ago, that cellulose is heterogeneous and attempted to explain the visible striations and certain types of lamellae as due to differences in water content. This hypothesis originated with Nägeli (23), who postulated water rich and water poor layers as a means of explaining concentricities and still permitting growth by intussusception. Differences in water content apparently do exist, and may be a factor influencing the intensity of birefringence in different lamellae. However, it is difficult to evaluate such differences by a study of dried material. Drying the walls shrinks the cell so that structures just within the limits of microscopic visibility when the preparation is in water, may be contracted to invisible dimensions. Furthermore, differences in water content must be explained in terms of submicroscopic differences in the cellulose which permit varying degrees of hydration. The question whether the variation in birefringence of different complexes of the cellulosic matrix is due to fluctuations in the size, number, or orientation of submicroscopic units of cellulose is one which must be attacked from the physical and chemical, rather than from the botanical, side.

C. SIGNIFICANCE OF BIOLOGICAL VARIABLES IN PHYSICAL AND CHEMICAL INVESTIGATIONS

Our survey of a wide range of gymnosperms and angiosperms indicates that the secondary wall is a very complex structure, and that the structural pattern of the cellulose matrix varies greatly, not only in different groups of plants but also, at times, in homologous cells of the same plant,

and even in different parts of the same cell. There is a similar variability in the distribution of "lignin" and of other non-cellulosic constituents. Therefore, since all types of secondary walls can not be homologized in a single structural model, there are grave dangers in generalizing from intensive investigations of isolated species, e.g., cotton, spruce, bamboo, or ramie.

Deductions concerning the structure of the cell wall based upon physical or chemical analyses, should be checked by microscopic investigations and by accurate information concerning the numerous biological variables. This is particularly necessary in the interpretation of X-ray diagrams, where the investigator of necessity must deal with complex aggregates of plant material. Van Iterson (31) has shown that certain misconceptions regarding *Valonia* might have been avoided by an acquaintance with the work of Correns (6) and others upon the visible structure of the walls of algae. Preston (25) undoubtedly errs in concluding, from an examination of X-ray diagrams, that there is a single plane of orientation of "fibrils" in the secondary wall of the tracheids of *Sequoia* and of other conifers. Accurate interpretations of X-ray diagrams of growing cells and of differentiating tissues are especially difficult, and such conclusions regarding structural changes as those of Clark and Farr (4) and Ritter and Stillwell (28) must be carefully verified from the histological side.

Although "lignin" residues of thick sections exhibit rod double refraction, as demonstrated by Freudenberg and his co-workers (12), a careful study of the residues of thin sections shows that a considerable proportion of the secondary wall "lignin" is isotropic. Similarly, there are parts of the cellulosic matrix which do not exhibit a clearly defined dichroism when thin sections are stained with chloro-iodide of zinc or congo red. The woods of certain dicotyledons leave no coherent structural residue when subjected to standard treatments with 72% sulphuric acid, as shown by Harlow (14); whereas others leave compact residues such as have been considered to be typical of conifers. In the wood of certain plants, the bulk of the "lignin" is confined to the so-called middle lamella, as Ritter (27) maintains; whereas in others, there is a relatively large proportion in the secondary wall.

It should be emphasized, in conclusion, that most of our own data were obtained from a study of tracheary cells and fibers, and that many additional types of cells must be investigated before it will be possible to visualize the full range of structural variability of the secondary wall. In a succeeding paper, we shall discuss methods that have been perfected for studying the small-celled, lightly lignified woods of dicotyledons of temperate regions.

SUMMARY AND CONCLUSIONS

1. An extensive survey of a wide range of gymnosperms and angiosperms has shown that the structural pattern of the secondary wall is clearly visible in the large fiber-tracheids and libriform fibers of various dicotyledons.

2. By using untreated sections of such cells as controls, it is possible to observe the exact effects of specific chemical and mechanical treatments upon normal structures, and thus to extend the scope of investigation to cover a wide range of less favorable material.

3. The cellulosic matrix of the swollen secondary wall of cotton, as of normal tracheids, fiber-tracheids, and libriform fibers, is an extremely heterogeneous but firmly coherent structure, the finer details of which grade down to the limits of microscopic visibility.

4. There is no reliable evidence to indicate that the matrix is composed of discrete entities of visible size — e.g., elementary fibrils, dermatosomes, ellipsoidal bodies, etc. — that are bound together by non-cellulosic material. On the contrary, our data demonstrate that such putative entities actually are heterogeneous fragments that are shredded or disrupted from an originally continuous and coherent matrix. If there are discontinuities in the structural pattern of the cellulose in normal tracheary cells, they are confined to the submicroscopic field, e.g., to the realm of micelles or molecular chains.

5. The visible structural pattern of the cellulosic matrix varies greatly in form and texture, not only in different plants, but also in homologous cells of the same plant, and even in different parts of the same cell.

6. There are at least two optically different elongated complexes of cellulose which may be segregated into radio-helical, radio-longitudinal, or concentric-longitudinal lamellae, or into various radio-concentric patterns.

7. The orientation of the elongated complexes of the structural pattern fluctuates more or less in successively formed parts of the secondary wall. In the case of normal tracheids, fiber-tracheids, and libriform fibers, there are three layers due to varying orientations: narrow inner and outer layers, in which the orientation is more nearly at right angles to the longitudinal axis of the cell, and a central layer of varying width, in which the orientation is parallel to this axis or does not deviate excessively from it.

8. "Lignin" and other non-cellulosic constituents may be deposited in the elongated, intercommunicating interstices of the cellulosic matrix, thus resulting in two continuous, interpenetrating systems. In heavily

lignified forms, either system may be dissolved without seriously modifying the structural pattern of the remaining system. The purified cellulose and the "lignin" residue reveal positive and negative images of the original structural pattern.

9. Deviations from the typical 3-layered type of secondary wall are of not infrequent occurrence. Thus, many thick-walled libriform fibers and fiber-tracheids have no clearly differentiated inner layer; whereas others have more than three layers of varying "fibrillar" orientation.

10. Conspicuous discontinuities in the structural pattern of the cellulose commonly occur in the multiple-layered walls of so-called gelatinous fibers, in certain types of bast fibers, and in sclereids. They are due to narrow layers of truly isotropic material which contain little, if any, cellulose.

11. There are five different types of visible concentricities which occur in varying combinations, and may be associated at times with radio-helical or radio-longitudinal lamellae. Therefore, it is misleading and fruitless to attempt to homologize all types of fibers in a single structural model.

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DESCRIPTION OF PLATES

Figs. 1-6 and 13 were made from unstained sections and were photographed in polarized light between crossed nicols. All the remaining photomicrographs were made with an arc-light and Zettnow's filter. Figs. 1-6, 8, 10, and 21 were made from sections mounted in diaphane ($N = 1.47$).

PLATE 140

- Fig. 1. *Myodocarpus simplicifolius* Brong. & Gris. Transverse section of the xylem, showing a fiber-tracheid and parts of seven adjoining ones. The thick secondary walls are composed of three distinct layers: a narrow brilliant outer layer, a brilliant narrow inner layer, and a wide intervening dark layer. In a section of this thickness, $15\ \mu$, the isotropic intercellular substance and the feebly anisotropic primary walls are more or less completely fogged or obscured by the brilliant outer layers of the secondary walls (compare Fig. 3 for a section $5\ \mu$ in thickness). $\times 1750$.
- Fig. 2. *Urandra corniculata* Foxw. Radial longitudinal section of the xylem, showing the walls of adjacent fiber-tracheids in sectional view. The broad central layers of the secondary walls are brilliant. The intercellular substance, the feebly birefringent primary walls, and the inner and outer layers of the secondary wall are dark. A bordered pit is shown in the center of the photomicrograph. $\times 1750$.
- Fig. 3. *Trochodendron aralioides* Sieb. & Zucc. Transverse section of the xylem, showing a tracheid and parts of seven adjoining cells. In a section of this thickness, $5\ \mu$, the outer brilliant layers of the secondary walls of adjacent cells are clearly separated by a narrow intervening dark layer, which actually consists of two feebly birefringent primary walls and a truly isotropic layer of intercellular material. $\times 1400$.
- Fig. 4. *Myodocarpus simplicifolius*. Transverse section of the xylem, showing a fiber-tracheid and parts of seven adjoining ones. The thick secondary wall of the central cell consists of a series of alternating brilliant and dark layers. $\times 1750$.
- Fig. 5. *Urandra corniculata*. Thick secondary wall of a sclerenchymatous cell in sectional view, showing alternating brilliant and dark layers. $\times 1750$.

PLATE 141

- Fig. 6. *Pandanus odoratissimus* L. Transverse section of a group of lignified fibers, showing secondary walls composed of regularly alternating brilliant and dark layers. $\times 1150$.
- Fig. 7. *The same*. Transverse section of a fiber after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in balsam, showing residue of secondary wall. The brilliant layers of Fig. 6 are split and embossed. $\times 1300$.

PLATE 142

- Fig. 8. *Siparuna bifida* (P. & E.) A. DC. Transverse section of a fiber-tracheid and of parts of several adjoining cells, stained with Haidenhain's haematoxylin and safranin, showing zones of varying intensities of lignification. $\times 2000$.
- Fig. 9. *The same*. Transverse section of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's

haematoxylin and mounting in aniline oil, showing finely radio-reticulate pattern and zones due to varying intensities of lignification. Dark zones heavily lignified, light zones less intensely lignified. $\times 1300$.

PLATE 143

- Fig. 10. *Siparuna bifida*. Transverse section of a fiber-tracheid and of parts of several adjoining cells, stained with Haidenhain's haematoxylin and safranin. The broad, unswollen central layer of the secondary wall is radially striated. $\times 2000$.
- Fig. 11. *The same*. Transverse section of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing radially striated and finely reticulated residue of the central layer of the secondary wall. In the outer part of the central layer, there is a concentricity due to an abrupt transition from coarse to fine texture. The inner concentricity is due to varying intensities of lignification. $\times 1900$.

PLATE 144

- Fig. 12. *Tetramerista glabra* Miq. Tangential longitudinal section of the central layer of a fiber-tracheid after treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing longitudinal pattern of fine anastomosing threadlike components. The longitudinal orientation has been somewhat distorted during swelling. $\times 1900$.
- Fig. 13. *Siparuna bifida*. Tangential longitudinal section through the central layer of a fiber-tracheid mounted in water and photographed with polarized light between crossed nicols, showing alternating birefringent and isotropic striae. $\times 1900$.
- Fig. 14. *The same*. Transverse section of a delignified fiber-tracheid, after treatment with diluted cuprammonium hydroxide and staining with congo red. The denser, darker radii of the purified cellulose correspond to the lighter radii of *Figs. 10 and 11*. $\times 1200$.

PLATE 145

- Fig. 15. *Poraqueiba sericea* Tul. Transverse section of the secondary wall of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing concentrically lamellated residue of the central layer. $\times 3200$.
- Fig. 16. *Siparuna bifida*. Transverse section of the secondary wall of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin and mounting in aniline oil, showing finely radio-reticulate residue of the central layer. $\times 3200$.

PLATE 146

- Fig. 17. *Gossypium hirsutum* L. Transverse section of a cotton hair after swelling with diluted cuprammonium hydroxide and staining with congo red, showing alternating lamellae of varying width and porosity in the inner part of the secondary wall. A particle $1\ \mu$ in diameter in the untreated wall would expand to the size of the circle at (a). $\times 1200$. Owing to swelling, the original width of the lamellae has been increased 7500 times in this photomicrograph.

- Fig. 18. *Pinus ponderosa* Dougl. Transverse section of the secondary wall of a tracheid after treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing concentrically laminated residue of the central layer. $\times 1900$.

PLATE 147

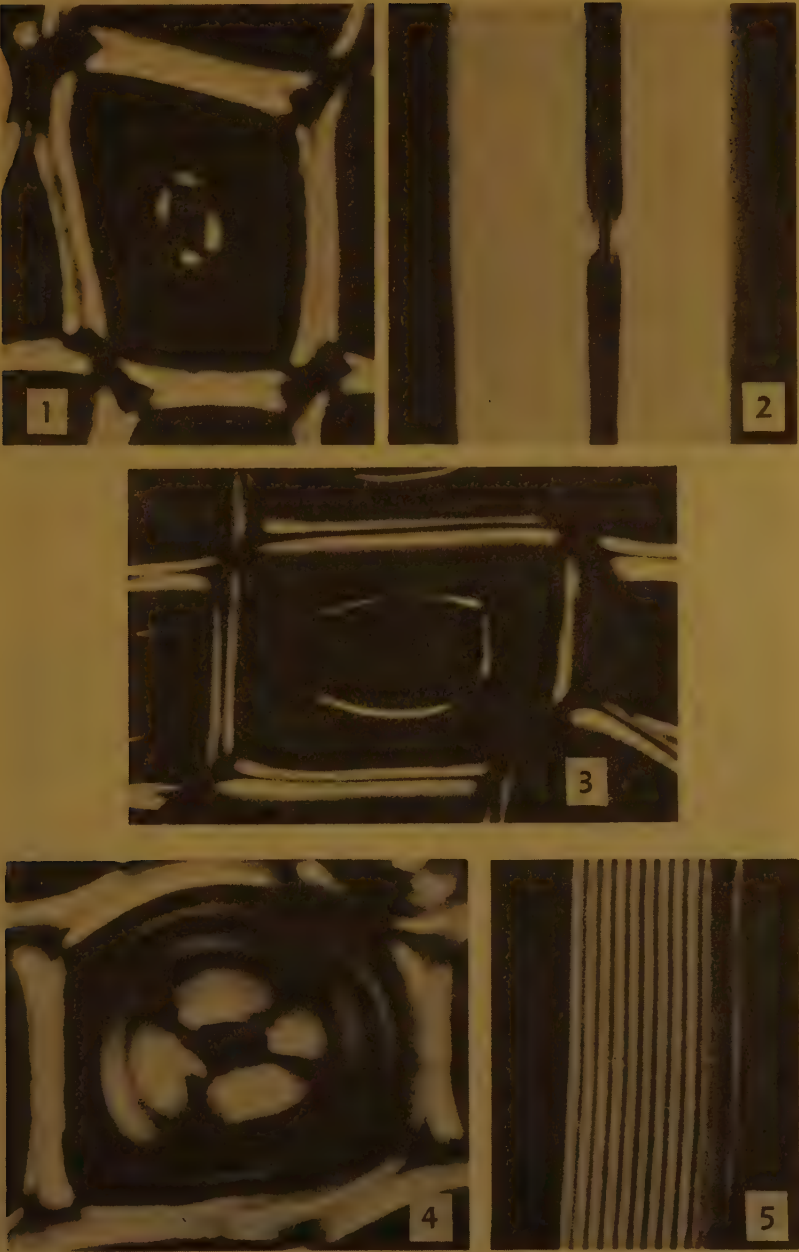
- Fig. 19. *Tetramerista glabra*. Transverse section of a fiber-tracheid and of parts of several adjoining cells, mounted in a dilute aqueous solution of iodine potassium iodide and photographed with a Zeiss 70-water-immersion lens. The broad central layer has a coarsely radio-concentric pattern which is complicated by zones of varying intensities of lignification. $\times 2000$.
- Fig. 20. *The same*. Transverse section of a fiber-tracheid after treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in balsam, showing finely radio-concentric pattern and broad zones due to varying intensities of lignification. $\times 1300$.

PLATE 148

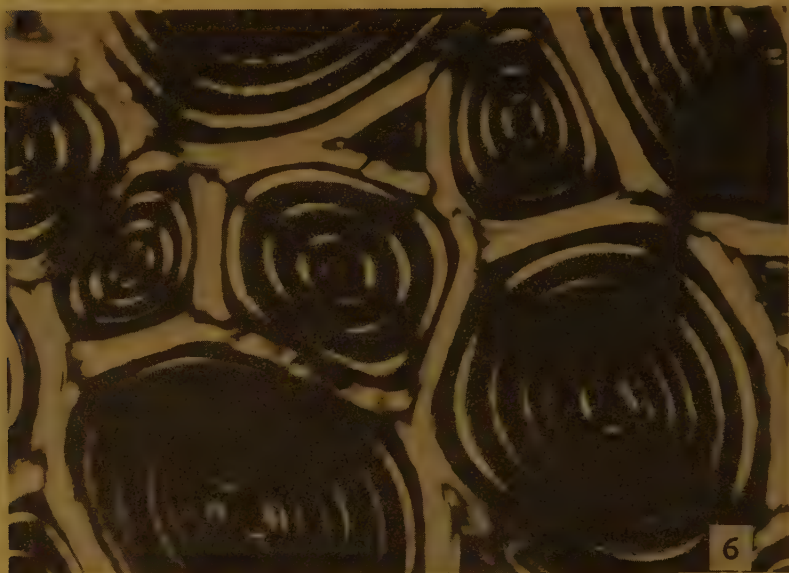
- Fig. 21. *Homalium luzoniense* F. Villar. Transverse section of a libriform fiber stained with Haidenhain's haematoxylin and safranin, showing alternating broad cellulosic and narrow non-cellulosic layers. The radio-reticulate structure of the former layers is vaguely visible. $\times 3200$.
- Fig. 22. *The same*. Transverse section of a libriform fiber after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline, showing residue of both the cellulosic and the non-cellulosic layers. $\times 1300$.

PLATE 149

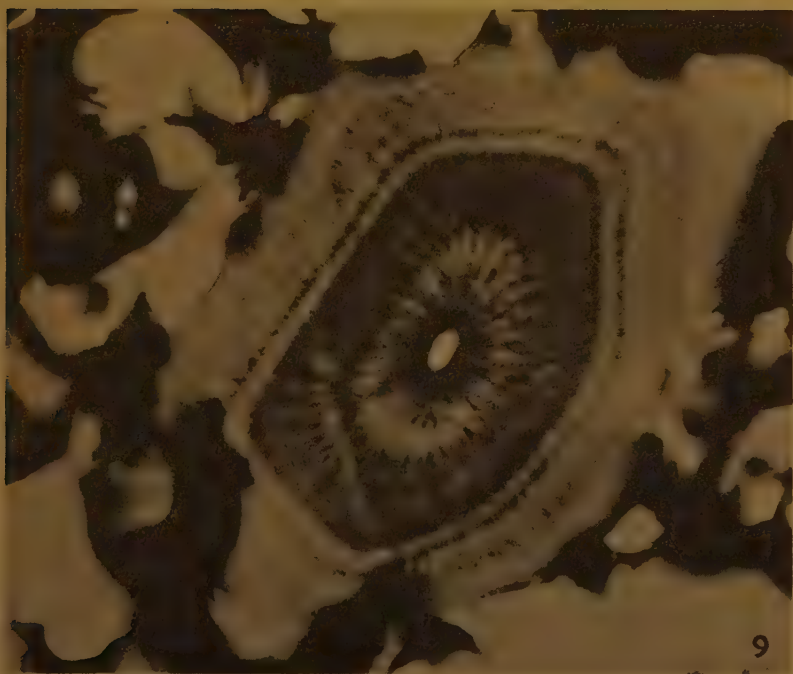
- Fig. 23. *Rhizophora mangle* L. Isolated, delignified, libriform fiber, swollen in diluted Schweizer's reagent, showing beadlike swelling of the central layer of the secondary wall. The outer layer of secondary wall is resolved into a series of constricting rings and helical bands. $\times 650$.
- Fig. 24. *Olmediella Betschleriana* (Goepp.) Loes. Isolated, delignified, libriform fiber, swollen in diluted Schweizer's reagent. The outer layer of the secondary wall is resolved into constricting helical bands. $\times 325$.
- Fig. 25. *Pandanus odoratissimus*. Isolated delignified fiber, swollen in diluted Schweizer's reagent, showing that each of the internal brilliant layers in Fig. 6 may be resolved into constricting rings and helical bands. $\times 650$.
- Fig. 26. *Olmediella Betschleriana*. Segment of a libriform fiber isolated from a thick transverse section of the xylem after delignification and treatment with 50% sulphuric acid. The concentric cylinders of cellulose are slipping apart. $\times 650$.
- Fig. 27. *Olmediella Betschleriana*. Isolated, delignified, libriform fiber, swollen in diluted Schweizer's reagent. The outer layer of the secondary wall is resolved into a series of constricting rings and helical bands. $\times 400$.



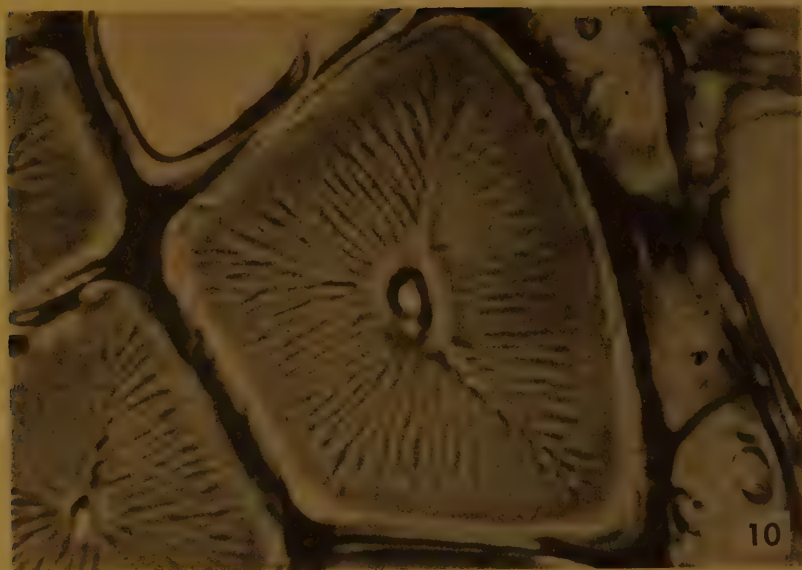
VISIBLE STRUCTURE OF THE SECONDARY WALL



VISIBLE STRUCTURE OF THE SECONDARY WALL



VISIBLE STRUCTURE OF THE SECONDARY WALL



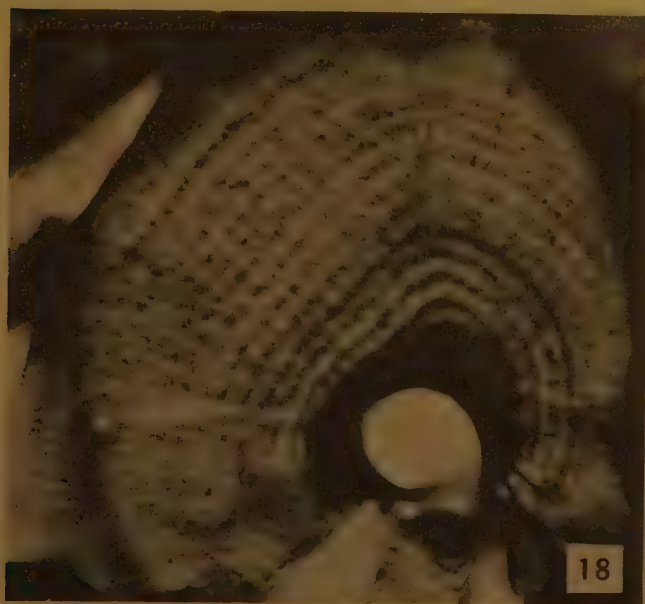
VISIBLE STRUCTURE OF THE SECONDARY WALL



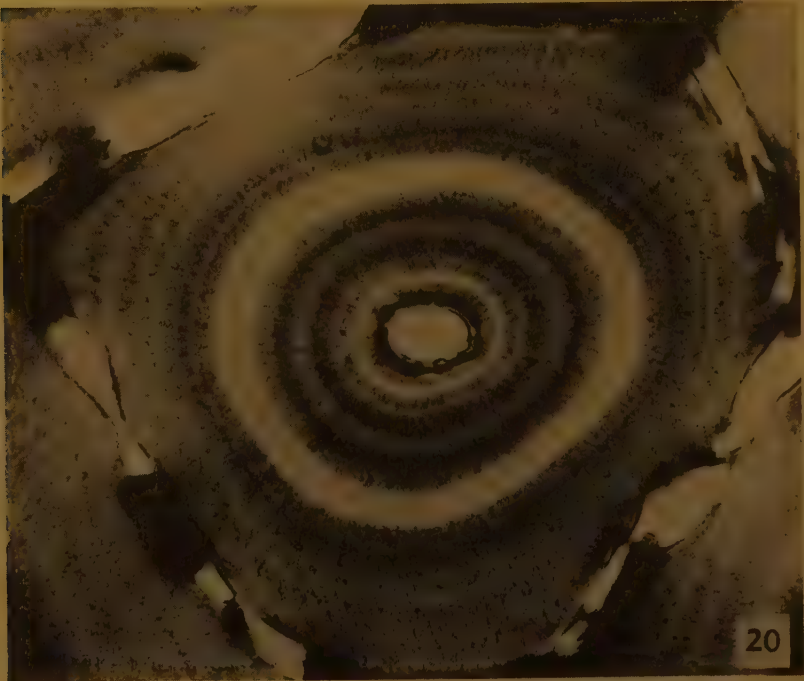
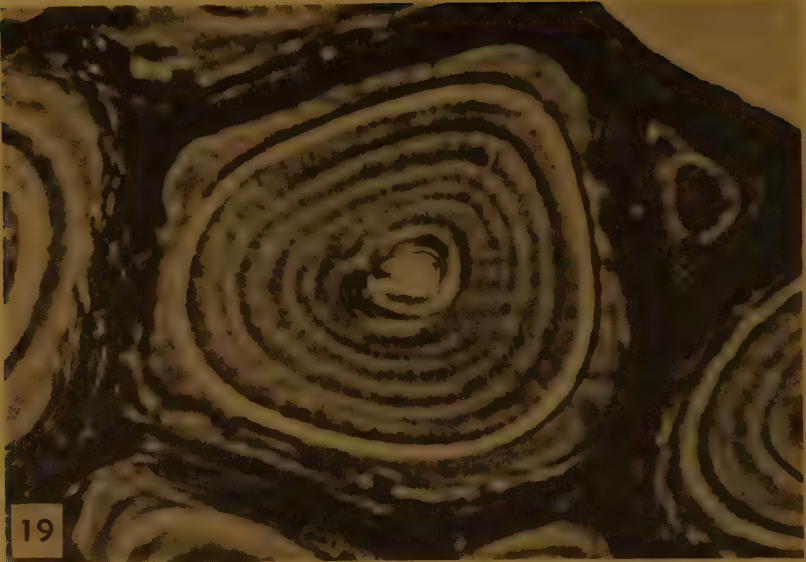
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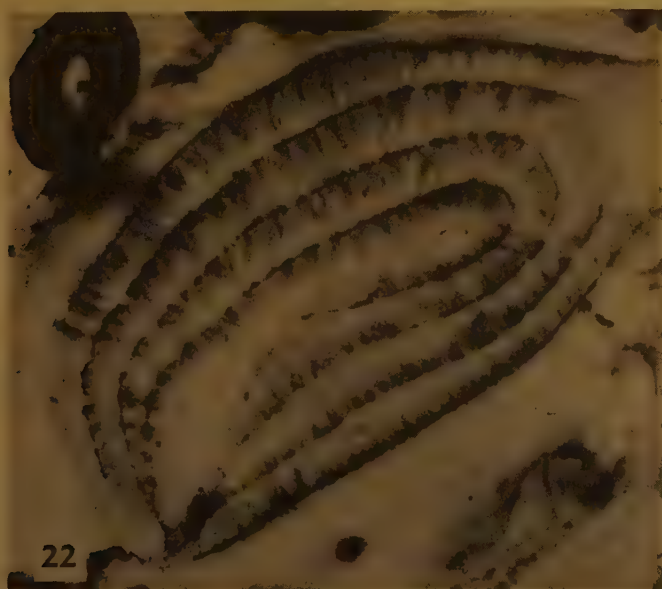
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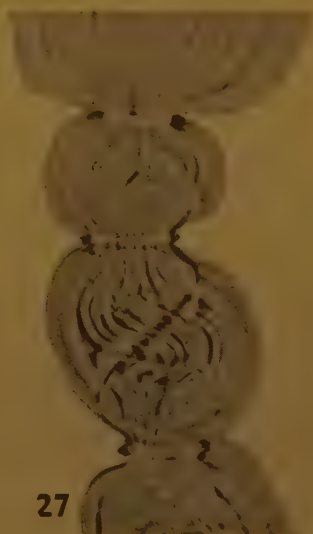
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THE EFFECT OF TEMPERATURE ON NUCLEAR DIFFERENTIATION IN MICROSPORE DEVELOPMENT

KARL SAX

With one text figure and plate 150

"HEREDITY is effected by the transmission of a nuclear preformation which, in the course of development, finds expression in a process of cytoplasmic epigenesis" (Wilson, 1925). The evidence from genetic and cytological investigations has proven conclusively that nuclear preformation is dependent upon the genic constitution of the chromosomes. The mechanism of expression in cytoplasmic epigenesis is more obscure. The problem is difficult because it is not subject to direct attack. A comparison of induced and hereditary effects has provided a method for studying certain developmental processes in *Drosophila*. An analysis of the effect of temperature on developing microspores has provided some information regarding nuclear cytoplasmic relations in differentiation and development, and has some bearing on the problem of genic expression.

Normal microspore development in *Tradescantia* has been described in detail by Sax and Edmonds (1933). The young microspore contains a centrally located nucleus surrounded by cytoplasmic granules. The granules disappear, and the nucleus migrates to the end of the oval-shaped microspore. The cytoplasm is massed around the nucleus, and at the other end of the cell there is a large vacuole. There is then a migration of cytoplasm and vacuole so that two vacuoles are formed, one at each end of the cell. Most of the cytoplasm lies between the vacuoles so that the longer axis of the cytoplasmic mass lies in the short axis of the cell. The nucleus at this time lies toward the heavy or dorsal wall of the microspore, — originally the inner wall at the time of tetrad formation. When the nucleus divides, the daughter nucleus near the heavy wall of the microspore is enclosed by a thin temporary wall which includes little cytoplasm. This nucleus does not pass into the typical resting stage, but retains its chromaticity and finally elongates to form the generative nucleus. The other nucleus formed near the center of the cytoplasmic mass enlarges to form the inactive tube nucleus. Shortly after the division of the microspore nucleus, the vacuoles disappear, and the cytoplasm appears to be rather homogeneous.

The normal development of the microspore of *Pseudolarix amabilis*

resembles that of *Pinus*, described in detail by Coulter and Chamberlain (1901). Soon after the release of the microspore from the wall of the microsporocyte, the wings develop rapidly on opposite ends of the spore towards the ventral side of the cell, while the dorsal side of the spore, which was formed during meiosis, becomes thickened. At the time of the first nuclear division, the nucleus lies near the dorsal wall surrounded by most of the cytoplasm, and the region towards the wings and the ventral side of the spore are more vacuolate. The first division occurs across the short axis of the microspore, and the nucleus near the dorsal wall is cut off and degenerates. The other nucleus divides again in the same axis, and another prothallial cell is cut off. The third division produces the generative nucleus and the tube nucleus of the mature pollen grain. The generative nucleus lies near the inner or dorsal wall of the pollen grain and is cut off by a thin wall which encloses little cytoplasm, while the large tube nucleus lies free near the center of the cell.

THE EFFECT OF TEMPERATURE ON NUCLEAR DIFFERENTIATION

Both high and low temperatures are effective in producing abnormal development in the microspores of *Tradescantia*. Plants were placed in a constant temperature chamber where the temperature was maintained at about 6°C. for the cold treatment, or at about 35°C. for the heat treatment. Three days' treatment was sufficient to produce abnormal development at either temperature range, and doubtless a shorter time would be effective at the higher temperature. The microspores were examined soon after exposure to abnormal temperatures, and for several subsequent days after they had been placed in the normal greenhouse environment.

Three types of abnormalities were produced. Under normal conditions, only two nuclei are formed in the pollen grain,—the generative nucleus and the tube nucleus. The tube nucleus normally does not divide and is inactive in further development. The heat treatment occasionally causes the tube nucleus to divide in *Tradescantia* (Figs. 1 and 2). The subsequent fate of the daughter nuclei is not known. Apparently no great deviation from normal environment is required to produce a second division, since this behavior was observed by Mr. R. H. Goodwin in *Tradescantia* plants grown in the greenhouse at the Biological Institute of Harvard University.

The second type of abnormality is produced by either cold or heat treatment. The polarity of the microspore is disturbed so that the nuclear division is no longer oriented across the short axis of the cell.

In extreme cases the division is at right angles to the normal axis, the daughter nuclei are not differentiated, and the temporary cell wall is formed across the center of the microspore (Fig. 3). In most cases there is partial differentiation of the daughter nuclei, but the more compact nucleus does not elongate to form the typical generative nucleus (Fig. 4). The degree of differentiation of the two nuclei is closely associated with the angle of division. With a smaller degree of variation from the normal axis of division there is increased differentiation of the generative nucleus (Fig. 5). In a single anther all degrees of differentiation are found, including the normal condition (Fig. 6).

In order to determine more accurately the relation between the angle of division and the differentiation of the nuclei, a statistical study was made. All microspores measured were from a single flower taken from a plant which had been kept at a temperature of about 36°C. for three days. Camera lucida drawings were made of 163 microspores selected at random among those which showed the two nuclei in the same focal plane. The angle between the normal axis of division across the short diameter of the microspore and the line drawn through the centers of the two nuclei was taken as the angle of division. The length of the outline of the "generative" nucleus was measured in millimeters. This work, as well as the tabulation and analysis of the data, was done by my wife, Dr. Hally Jolivet Sax. The relation between the angle of division and the length of the generative nucleus is shown in Table 1. The high correlation of $-0.81 \pm .02$ shows that the degree of nuclear differentiation is closely associated with the angle of division.

A third type of aberrant development was found in microspores which began to "germinate" before the division of the nucleus. In some cases one of the daughter nuclei was found in the original microspore and the other in the newly-formed outgrowth (Figs. 8 and 10). In these cases a thin cell wall divided the cytoplasm into approximately equal parts, and there was no indication of nuclear differentiation. The division may occur so that neither daughter nucleus remains in the original microspore (Figs. 7 and 9). If the division is oriented lengthwise of the cytoplasmic mass, there is no nuclear differentiation, but if it is oriented across the short diameter of the outgrowth, so that one daughter nucleus is near the cell wall, there is a differentiation which resembles that following normal division in a normal microspore (Fig. 7).

The precocious growth of the microspores of *Tradescantia* is unlike normal pollen-tube growth. The pollen-tube usually grows from the end of the pollen grain adjacent to the heavy dorsal wall, while the aberrant outgrowth occurs at the ventral side of the microspore. Per-

haps this abnormal growth is the first stage in the development of an embryo-sac-like structure such as Stow (1930, 1933) has found in the anthers of *Hyacinthus*. Unfortunately, a study of the further development of the abnormal growth in *Tradescantia* microspores could not be continued because the anthers dehisced and disintegrated so soon. Possibly these peculiar microspores could be developed further in a nutrient solution.

TABLE I.

THE RELATION BETWEEN ANGLE OF DIVISION AND THE DIFFERENTIATION OF THE NUCLEI IN MICROSPORES OF *TRADESCANTIA*

		Angle of division									
Length of generative nucleus		0	10	20	30	40	50	60	70	80	90
	8-11	2		1	2		2	2	3	3	3
	11				2	1	5	3	8	3	9
	14	1	1	3	1	1	4	2	2	2	
	17		5	4		3		3	2		
	20	4	7	7	2	2	2	1	1		
	23	10	4	5	1	1	1	1			
	26	9	3	3			1			1	
	29	3			1			1			
	32	3			1						
	35										
	38-40	4	1								

$$n = 163$$

$$r = -.81 \pm .02$$

The development and differentiation of the microspores of *Pseudolarix amabilis* is also affected by environmental conditions. Branches containing male flowers were placed in a warm corner of the greenhouse for about two weeks. During this time meiosis occurred, and the microspores developed to maturity. Most of the microspores were normal in their development (Figs. 11 and 12), but various types of abnormalities were observed. If the first division occurs lengthwise of the cell in the axis of the wings, there is no differentiation of the nuclei if each is an equal distance from the cell wall (Fig. 13). If, however, one nucleus lies near the cell wall, regardless of the orientation of the division spindle, this nucleus tends to remain small and form a prothallial cell, while the nucleus near the center of the cytoplasmic mass remains large and divides again (Figs. 14 and 16). The first division may occur in the normal position, but the second division may be aberrant in orientation (Figs. 15 and 16). Several years ago Mrs. Sax found a mature pollen grain of *Picea* which contained four undifferentiated nuclei of

approximately equal size. Apparently relatively slight changes in environmental conditions can cause abnormal development of conifer microspores. Nuclear differentiation in these microspores appears to be entirely dependent upon the orientation of the division spindles and the position of the nuclei in relation to the cytoplasmic mass.

Nuclear differentiation in the microspores of *Tradescantia* and *Pseudolarix* appears to be determined by the nuclear cytoplasmic relationships. In *Tradescantia* it is possible to observe the relations of nuclei, vacuoles, and cytoplasm in the living microspores. Observations at various stages of development show that normal development is dependent upon the synchronization of cytoplasmic and nuclear activities.

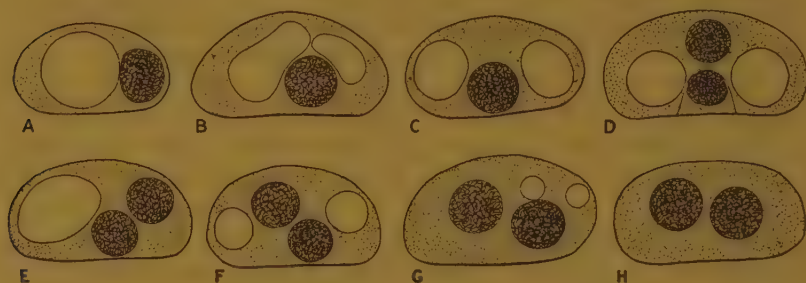
In the microspores which develop under normal conditions, the cell contents show a gradual shifting in position before the nucleus divides. A large vacuole is formed at one end of the microspore, and the nucleus and most of the cytoplasm move to the opposite end. The vacuole then extends towards the opposite end, near the ventral side of the spore, and finally forms two vacuoles, one at either end of the cell. Meanwhile the cytoplasmic mass and the nucleus migrate towards the center of the cell. The cytoplasm extends between the ventral and dorsal walls so that the length of the cytoplasmic mass is across the short diameter of the cell. Some cytoplasm extends around the entire periphery of the cell. The nucleus lies near the dorsal wall at the time of division. After the division the nucleus near the dorsal wall is cut off by a thin temporary wall, and then develops into the elongated generative nucleus. The other nucleus enlarges, loses its chromaticity, and becomes the inactive tube nucleus. The sequence of early development of the normal microspore is shown in text figures a, b, c, and d, which are camera lucida sketches drawn from living material.

When the microspore develops at low temperatures, the same cycle of development begins, but the nucleus divides before the vacuole, cytoplasm, and nucleus reach their normal positions. (Text figure e.) Since the cytoplasm migrates towards the center of the cell along the dorsal wall of the microspore, the length of the cytoplasmic mass is at an angle to the normal axis of division. The nuclear spindle is oriented in the long axis of the cytoplasmic mass, and the daughter nuclei lie towards one end of the microspore and do not undergo complete differentiation.

The exposure to high temperatures for several days appears to accelerate the cytoplasmic movement without causing a corresponding activity of the nucleus. At the time the cell constituents are in the position usually associated with nuclear division (Text figure c), the nucleus may remain inactive. The vacuoles then become smaller or may dis-

appear entirely before nuclear division. As a result, the long axis of the cytoplasmic mass is not oriented in the short axis of the cell, and the division may occur at various angles, depending in part upon the cytoplasmic distribution (Text figures f, g, and h).

In a single flower, following heat treatment, the angle of division may vary from 0 to 90 degrees. Camera lucida drawings were made from a random sample of these cells, and the angle of division was determined in relation to the distribution of cytoplasmic mass. The length of the



TEXT FIGURE. Development of the microspore under normal and abnormal conditions.

All figures are from camera lucida drawings of living microspores.

Figures a, b, c, and d show the movement of the cell contents during early development of the microspore under normal conditions. The vacuole becomes extended along the ventral wall and finally forms two vacuoles. The nucleus at the time of division becomes oriented near the dorsal or heavy wall of the microspore.

Figure e shows the nuclei formed by nuclear division before normal orientation of the cell constituents is attained. This microspore developed at a low temperature, which seems to retard cytoplasmic movement without retarding nuclear division.

Figures f, g, and h are drawings of microspores which had been subjected to a high temperature. The vacuoles are small or absent at the time of nuclear division, and the axis of division tends to occur in the long axis of the cytoplasmic mass.

cytoplasmic mass was determined for the long axis of the cell, and the width was measured across the short axis of the cell. For example, in a normal microspore (fig. d) the length of the cytoplasmic mass is the distance between the vacuoles, and the width is the distance across the microspore in the axis of division, and the angle of division is very small. In this cell the length-width ratio is about 0.5. In figure e the length-width ratio is about 1.0, and the angle of division is about 45 degrees, while in figure h the length-width ratio of the cytoplasmic mass is about 2.0, and the angle of division is about 80 degrees. The length-width

ratio of the cytoplasmic mass correlated with the angle of division gave a value of $r = .66 \pm .03$. It is evident that there is a strong tendency for the nucleus to divide in the long axis of the cytoplasmic mass, although as the volume of cytoplasm increases, there is not a corresponding tendency for the nucleus to divide in the longer axis. In general, however, the direction of division in the microspore is controlled by the distribution of the cytoplasm in accord with Hertwig's rule, and the nuclear differentiation is controlled by the position of the daughter nuclei in relation to the cytoplasmic mass.

It is not possible to follow the cytoplasmic movements in the living cells of conifers, but judging from the description of normal development (Ferguson, 1904) and the behavior of the nuclei in abnormal microspores, the failure of normal differentiation is also based on the disturbed relations of nucleus, cytoplasm, and vacuoles.

A comparison of nuclear differentiation in *Tradescantia* and *Pseudolarix* microspores and in the embryo sacs derived from microspores in *Hyacinthus* shows a good deal of similarity in polarity. In both *Tradescantia* and *Pseudolarix* the center of activity in early microspore development is near the dorsal wall which was formed during microsporogenesis. If a second division occurs in the *Tradescantia* microspore, the nucleus nearer the center of the cell divides, as is the case in normal microspore development in the conifers. The vegetative nucleus is always the one nearer the ventral wall and is surrounded by a large amount of cytoplasm, while the generative or sexual nucleus lies near the dorsal wall and is enclosed by a thin temporary cell wall which includes little cytoplasm. The "embryo sacs" which develop from microspores of *Hyacinthus* (Stow, 1933) show the exine of the microspore at the egg or sexual end of the embryo sac, while the polar or vegetative nuclei lie in the center of the embryo sac, apparently surrounded by a relatively large amount of cytoplasm.

Stow was able to induce embryo sac-like structures in anthers of *Hyacinthus* by subjecting the bulbs to a temperature of 28°C. for 18 to 24 hours at the time of planting in the fall. The abnormal development observed in the following spring may have been induced either by the temperature treatment or by the effects produced by the large number of degenerating sterile microspores. At any rate the differentiation of the microspore to produce a normal pollen grain or an embryo sac appears to depend upon environmental conditions. We are inclined to believe that the precocious growth of *Tradescantia* microspores is the first stage in embryo sac formation, and that the complete structure could be developed, under temperature control, if the cells could be kept alive over a long period of time, as is the case in *Hyacinthus*.

FACTORS IN DEVELOPMENT AND DIFFERENTIATION

According to Osterhout (1921), life is dependent upon a series of reactions which normally proceed at rates which bear a definite relation to each other. If for life we substitute development and differentiation, we have an hypothesis which seems to explain development and differentiation. Certainly the differentiation of the microspore nuclei appears to be dependent upon the relative rates of cytoplasmic migration and nuclear activity. Less direct evidence indicates that the difference between a pollen grain and an embryo sac may be dependent upon the same type of timing relationships. If sex can be determined by the timing relationships of different reactions, effected either by environmental conditions or hereditary factors, we have indirect evidence that genic expression may be effected by differential reactions.

More direct evidence regarding the mechanism of genic expression is found in the behavior of the chromosomes at meiosis. A failure of chromosome pairing, or asynapsis, may be caused by genetic factors or by environmental conditions. Genetic asynapsis has been found in *Drosophila*, *Zea*, *Triticum*, *Rumex* and *Datura*. Induced asynapsis can be effected in *Rhoeo* and *Datura* by subjecting the plants to low temperatures for several days, and it has been obtained in *Tradescantia* following treatment at low and high temperatures. Both the hereditary and induced effects are similar in their expression. The chromosomes are unpaired at meiosis, the divisions are irregular, diploid gametes may be produced, and there is a high degree of pollen sterility in the asynaptic plants. Both types of asynapsis may be attributed to the same cause. If chromosome development is not synchronized with other cell activities, the chromosomes may not be effectively paired before nuclear division is initiated.

An exceptionally clear case of the timing factor in genic activity was found in *Aquilegia* by Anderson and Abbe (1933). The "compacta" mutant of *Aquilegia* is dependent on a single genetic factor. In the mutant type the branches are more erect and numerous, and the flowers are upright from the beginning. The dwarf type is caused by the precocious thickening of the cell walls, and the somatic expression is simply the result of disturbed timing relationships, — "the precocious initiation of a normal feature of normal development." Further aspects of the relation between genes and development in *Drosophila* have been discussed by Schultz (1935) and by Goldschmidt (1935), and similar work is being done on the cucurbits by Sinnott (unpublished).

The temperature chambers used in this work were paid for, in part, by a grant from the American Academy of Arts and Sciences.

SUMMARY

The subjection of *Tradescantia* plants to low and high temperatures may produce three kinds of abnormalities in microspore development. (1) The tube nucleus, which in normal microspores is inactive and ultimately degenerates, may divide. (2) The polarity of the cell may be disturbed so that the division of the microspore nucleus is not oriented in the normal axis. The angle of deviation is closely correlated with the differentiation of the daughter nuclei. (3) The microspore may become greatly extended on the ventral side, and the nuclear division may occur in this new outgrowth. This abnormality may be the first step in the transformation of a microspore to an "embryo sac," as found in *Hyacinthus* by Stow.

When *Pseudolarix* microspores are developed at a relatively high temperature, there is a failure of normal differentiation of the nuclei. The differentiation of prothallial cells and generative and tube nuclei is dependent upon the nuclear cytoplasmic relationships in the developing microspore.

The normal differentiation in *Tradescantia* microspores is dependent upon the synchronization of cytoplasmic movements and nuclear activity. There is some evidence that many differences in development and differentiation, induced either by genetic factors or by environmental conditions, are dependent upon differences in reaction rates of different processes.

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DESCRIPTION OF PLATE 150

Photographs of aceto-carmin preparations of abnormal microspores of *Tradescantia* and normal and abnormal microspores of *Pseudolarix amabilis*. Figures 1 to 6 inclusive, magnified $\times 800$. The other figures are magnified $\times 600$.

TRADESCANTIA

Figures 1 and 2. Division of the tube nucleus of the microspore.

Figure 3. The division of the microspore nucleus has occurred at right angles to the normal axis of division, and the daughter nuclei do not become differentiated.

Figures 4, 5, and 6. The nuclear divisions have occurred at various angles followed by a corresponding amount of nuclear differentiation. These microspores were developed at a high temperature.

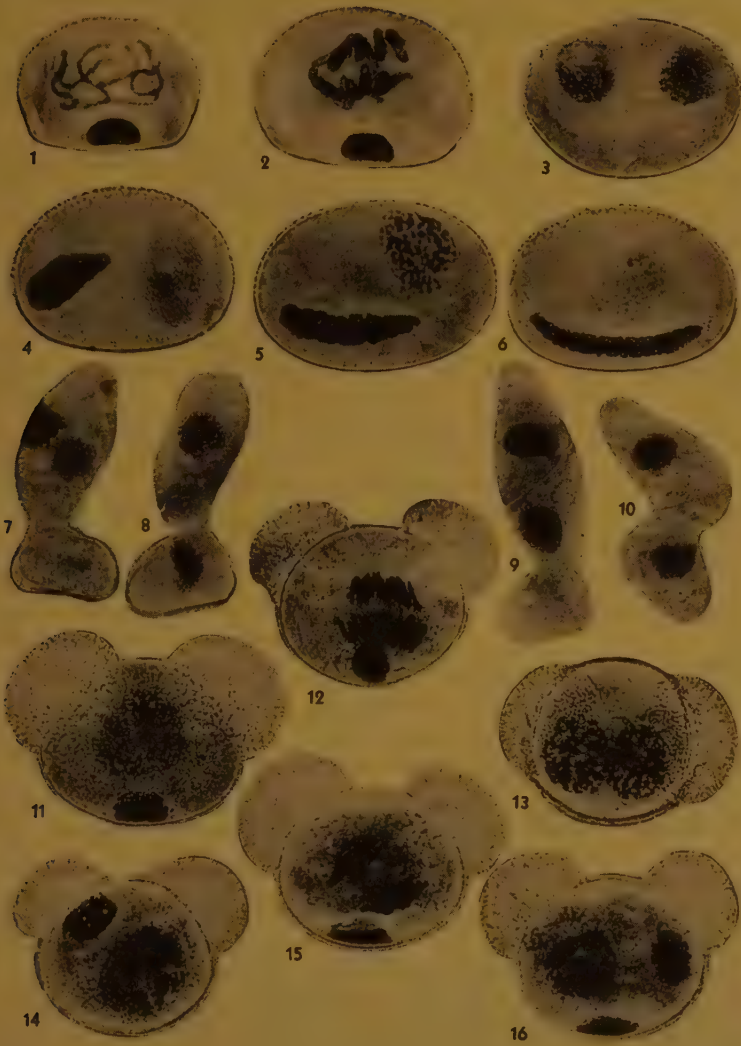
Figures 7, 8, 9, and 10. Abnormal microspores produced by heat and cold treatment.

PSEUDOLARIX

Figures 11 and 12. Stages in the normal development of the microspore. All divisions are across the short axis of the cell, and the prothallial cells are always cut off near the heavy dorsal wall.

Figures 13, 14, 15, and 16. Abnormal development induced by heat treatment. The nuclei may divide at various angles followed by various degrees of differentiation of the daughter nuclei. The prothallial cells may be cut off at any point along the cell wall.

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TEMPERATURE AND NUCLEAR DIFFERENTIATION

NOTES ON THE LIGNEOUS PLANTS DESCRIBED BY LEVEILLE FROM EASTERN ASIA¹

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LABIATAE

Leucosceptrum sinense Hemsley in Jour. Linn. Soc. Bot. **26**: 310 (1890). — Léveillé, Fl. Kouy-Tchéou, 209 (1914). — Dunn in Not. Bot. Gard. Edinb. **8**: 171 (1913); **6**: 192 (1915).

Elsholtzia Cavaleriei Léveillé & Vaniot in Fedde, Rep. Spec. Nov. **8**: 424 (1910).

Leucosceptrum Bodinieri Léveillé in op. cit. **9**: 224 (1911).

CHINA. K w e i c h o u : environs de Tsin-gay, au bord d'une rivière, *E. Bodinier*, no. 2709, Sept. 20, 1899 "sous -arbrisseau, fl. roses" (syntype of *Elsholtzia Cavaleriei*; photo. in A. A.); environs de Touchan, *J. Cavalerie* in herb. *Bodinier*, no. 2710, Sept. 1899 (syntype of *Elsholtzia Cavaleriei*; photo. in A. A.).

The name *Elsholtzia Cavaleriei* was changed by Léveillé to *Leucosceptrum Bodinieri* and later the two type specimens were enumerated by him in his Flore du Kouy-Tschéou under *L. sinense* without citation of synonymy, the reduction being based on identifications made by Dunn, to whom Léveillé had sent material of his Labiatae for revision, as it appears from a note in Léveillé's Flore du Kouy-Tchéou p. 203 under Labiacées which reads "(D. Dunn revisit)."

Leucosceptrum plectranthoideum (Lévl.) Marquand in Kew Bull. Misc. Inform. **1930**: 207.

Buddleia plectranthoidea Léveillé, Cat. Pl. Yun-Nan, 171 (1916).

CHINA. Y u n n a n : pâtures des montagnes à Pé-long-tsin, 3200 m., *E. E. Maire*, Nov. 1912 (holotype of *Buddleia plectranthoidea*; merotype in A. A.).

This species seems nearest to *L. sinense* Hemsl. but can be at once distinguished by the shorter inflorescence, the yellowish closer tomentum of the calyx and the bracts, and the shorter elliptic or ovate-elliptic to oblong-elliptic leaves reticulate beneath and tomentulose above.

Colquhounia Seguini Vaniot in Bull. Acad. Intern. Géog. Bot. **14**: 165 (1904). — Rehder in Sargent, Pl. Wilson. **3**: 380 (1916). —

¹Continued from Vol. **15**: 326; for preceding parts see Vol. **10**: 108-132, 164-196; **12**: 275-281; **13**: 299-332; **14**: 223-252; **15**: 1-27, 117.

Léveillé, Cat. Ill. Seu-Tchouen, 92, pl. 44 (1918). — P'ei, Verben. China in Mem. Sci. Soc. China, 1 (no. 3): 180 (1932).

Colquhounia elegans Wall. var. *pauciflora* Prain in Jour. As. Soc. Beng. 62: 38 (1893). — Dunn in Not. Bot. Gard. Edinb. 6: 179 (1915).

Caryopteris fluminis Léveillé, Sert. Yunn. 3 (1916); Cat. Pl. Yun-Nan, 298 (1917). — P'ei, Verben. China in Mem. Sci. Soc. China, 1 (no. 3): 180 (1932).

CHINA. K w e i c h o u : environs de Ou-la-gay (Tchin-lin), *J. Seguin* in herb. *Bodinier*, no. 2237, March 1898 "longues tiges sous-ligneuses, lianeuses" (syntype of *C. Seguni*; photo. in A. A.); rives du fleuve Bleu, alt. 450 m., *E. E. Maire*, June 1912, "petit arbuste, feuilles persistantes, fleurs roses" (holotype of *Caryopteris fluminis*; photo. in A. A.). Y u n n a n : environs de My-tsao, *Fr. Ducloux*, no. 110, March 4, 1897, "long tiges s'enlaçant aux arbres et buissons, fleurs coccinées, 4 graines ailées" (syntype of *C. Seguni*; photo. in A. A.).

By Dunn (l. c.) this species was referred to *C. elegans* var. *pauciflora* Prain, but as I pointed out in 1916 (l. c.) this variety is best considered a distinct species which becomes *C. Seguni* Vaniot.

Micromeria biflora Benthams, Labiat. 378 (1834). — Dunn in Not. Bot. Gard. Edinb. 6: 157 (1915). — Léveillé, Fl. Kouy-Tchéou, 210 (1914); Cat. Pl. Yun-Nan, 138 (1916).

Thymus Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. 11: 298 (1912).

CHINA. K w e i c h o u : Tin-lan, montagnes sablonneuses, *J. Cavalerie*, no. 3778, "blanc-rose" (syntype of *Thymus Cavaleriei*; photo. in A. A.). Y u n n a n : Pan-pien-kai, pâturages des coteaux calcaires, alt. 2550 m., *E. E. Maire*, Sept. 1911 "Thymus vivace, étalé, fl. roses" (syntype of *Thymus Cavaleriei*; photo. in A. A.).

Elsholtzia rugulosa Hemsley in Jour. Linn. Soc. 26: 278 (1890). — Léveillé, Fl. Kouy-Tchéou, 208 (1914); Cat. Pl. Yun-Nan, 138 (1916). — Dunn in Not. Bot. Gard. Edinb. 6: 149 (1915).

Elsholtzia Labordei Vaniot in Bull. Acad. Intern. Géog. Bot. 14: 177 (1904).

CHINA. K w e i c h o u : environs de Tsin-gay, à Tchao-see, abonde dans la mont. et bord de routes, *J. Laborde* in herb. *Bodinier*, no. 2711, Sept. 7, 1899 "fleurs d'un bleu très pâle" (holotype of *E. Labordei*; photo. in A. A.).

Elsholtzia fruticosa (D. Don) Rehder in Sargent, Pl. Wilson. 3: 381 (1916).

Elsholtzia polystachya Benthams, Labiat. 116 (1832). — Dunn in Not.

Bot. Gard. Edinb. 8: 161 (1913); 6: 149 (1915). — Lévillé, Fl. Kouy-Tchéou, 208 (1914); Cat. Pl. Yun-nan, 138 (1916).

Elsholtzia tristis Lévillé in Fedde, Rep. Spec. Nov. 8: 424 (1910).

Elsholtzia Dielsii Lévillé in op. cit. 9: 441 (1911).

Elsholtzia Souliei Lévillé in op. cit. 9: 248, non p. 218 (1911).

CHINA. Szechuan: Ta-tsien-lu, *J. A. Soulié*, nos. 781 and 1023, in 1893 (syntypes of *E. Dielsii* [*E. Souliei* Lévl. p. 248, non p. 218]; photos. in A. A.). Kweichou: environs de Kouy-yang, mont du Collège, *E. Bodinier*, no. 1944, Nov. 3, 1897, "tige 1 m., fleurs blanches" (holotype of *E. tristis*, photo. in A. A.).

Elsholtzia ochroleuca Dunn in Not. Bot. Gard. Edinb. 8: 161 (1913).

Elsholtzia lampradena Lévillé in Bull. Géog. Bot. 25: 25 (1915); Cat. Pl. Yun-Nan, 137 (1916). — **Synon. nov.**

CHINA. Yunnan: pâturages des collines à Tong-tchouan, alt. 2600 m., *E. E. Maire*, Sept. 1912 "arbrisseau rameux, haut 0.40 m., fleurs blanches en épis dressés" (holotype of *E. lampradena*; photo. in A. A.).

Elsholtzia lampradena has been identified with *E. ochroleuca* according to a note on the type specimen.

Pogostemon glaber Benthham in Wallich, Pl. As. Rar. 1: 31 (1830). — Lévillé, Cat. Pl. Yun-Nan, 143 (1916).

Caryopteris Esquirolii Lévillé in Fedde, Rep. Spec. Nov. 9: 449 (1911); Fl. Kouy-Tchéou, 440 (1915). — **Synon. nov.**

CHINA. Kweichou: Tchou-ly, alt. 900 m., *J. Esquirol*, no. 2053, March 1, 1910, "fl. blanche, labelle rose" (holotype of *Caryopteris Esquirolii*; merotype in A. A.).

Pogostemon glaber has not yet been recorded from Kweichou, as far as I know, but it is known from Yunnan.

Plectranthus ternifolius Don, Prodr. Fl. Nepal. 117 (1825). — Lévillé, Fl. Kouy-Tchéou 214 (1914); Cat. Pl. Yun-Nan 143 (1916). — Dunn in Not. Bot. Gard. Edinb. 6: 138 (1915).

Elsholtzia Lychnitis Lévillé & Vaniot in Fedde, Rep. Spec. Nov. 8: 425 (1910).

Teucrium Esquirolii Lévillé in Bull. Géog. Bot. 22: 236 (1912).

CHINA. Kweichou: Tchen-lin-tchéou, route de Lo-pie à Oula-gay, *L. Martin* in herb. *Bodinier*, no. 1937, Oct. 9, 1899, "tige de 1.50 m. de haut, fleur blanches, ou blanc-bleuâtre" (syntype of *Elsholtzia Lychnitis*; photo. in A. A.); route de Tou-tchéou à Pien-yang, *J. Cavalerie*, no. 2573, Nov. 1905 (syntype of *E. Lychnitis*; photo. in A. A.); coteaux de Lo-fou, *J. Esquirol*, no. 2576, Nov. 1910 (holotype of *Teucrium Esquirolii*; ex Lévillé).

Of *Teucrium Esquirolii* I have seen no specimen, but Lévillé enumerates it in 1916 (Cat. Pl. Yun-Nan, 143) as a synonym of *Plectranthus ternifolius*, probably on identification by S. T. Dunn, though Dunn does not cite it in 1915. It does not appear in the Flore du Kouy-Tchéou. *Plectranthus ternifolius* should probably not be classed as a ligneous plant, though Hooker describes it in his Flora of British India (4: 621) as a bush 3-5 ft. high.

Plectranthus coetsa Hamilton ex Don, Prodr. Fl. Nepal. 117 (1825). — Lévillé, Cat. Pl. Yun-Nan, 141 (1916).

Plectranthus Mairei Lévillé, Cat. Pl. Yun-Nan, 141 (1916), pro synon. *P. coetsa* Ham.

CHINA. Y u n n a n : pâturages des mont. derrière Tong-tchouan, 2700 m., *E. E. Maire*, Oct. (1912-13), "plante annuelle très-rameuse, fl. rouge vif" (type of *P. Mairei*; photo. in A. A.); haies, plaine de Tché-hay, 2550 m., *E. E. Maire*, Sept. [1912-13], "plante vivace, tumescente, en touffes, haut 1.40 m." (in herb. Lévillé with *P. Mairei*; photo. in A. A.).

Plectranthus Mairei is apparently an unpublished name and is cited only as a synonym of *P. coetsa* (l. c.). On Mairei's specimen from Tong-tchouan the name *Plectranthus Mairei* appears in Lévillé's handwriting; the specimen from Tché-hay is without any name, but placed in the cover of *P. Mairei*.

The majority of Labiatae described by Lévillé are herbaceous and most of them have been examined by S. T. Dunn. He published his identifications in his Notes on Chinese Labiatae (in Not. Bot. Gard. Edinb. 8: 153-171. 1913) and in his Key to the Labiatae of China (op. cit. 6: 127-208. 1915). The identifications and reductions made by Dunn were accepted by Lévillé and incorporated in his Flore du Kouy-Tchéou (p. 203-217) and in his Catalogue des plantes de Yun-Nan (p. 136-149).

SOLANACEAE

Solanum aculeatissimum Jacquin, Coll. 1: 100 (1786); Ic. Rar. 1: t. 41 (1781-86). — Merrill in Contr. Arnold Arb. 8: 149 (1934).

Solanum Bodinieri Lévillé & Vaniot in Bull. Soc. Bot. France, 55: 206 (1908).

Solanum Cavaleriei Lévillé & Vaniot, l. c. 207 (1908). — **Synon. nov.**

CHINA. H o n g k o n g : plage sablonneuse de l'île Verte, *E. Bodinier*, July 31, 1895 (holotype of *S. Bodinieri*; photo. in A. A.). K w e i c h o u : Ly-po-hien, *J. Cavalerie* in herb. *Bodinier*, no. 2722, Aug. 10, 1899 (holotype of *S. Cavaleriei*; photo. in A. A.).

Solanum Bodinieri represents a glabrescent form of this very variable

species, while *S. Cavaleriei* is much more pubescent throughout. *Solanum Bodinieri* has been identified with *S. aculeatissimum* by Merrill (l. c.).

SCROPHULARIACEAE

Brandisia racemosa Hemsley in Kew Bull. Misc. Inform. 1895: 114.

Deutzia funebris Léveillé, Sert. Yunn. 1 (1916). — Cat. Pl. Yun-Nan, 296 (1917). — **Synon. nov.**

CHINA. K w e i c h o u : rives du fleuve Bleu à Kiang-pien, alt. 350 m., *E. E. Maire*, Aug. 1913, "arbuste un peu grimpant; fl. roses" (holotype of *Deutzia funebris*; merotype in A. A.).

BIGNONIACEAE

Incarvillea Delavayi Bureau & Franchet in Jour. de Bot. 5: 138. (1891).

Tecoma Mairei Léveillé, Cat. Pl. Yun-Nan, 20 (1916). — **Synon. nov.**

CHINA. Y u n n a n : rochers sous brousse, mont. de Pe-long-tsin, alt. 3200 m., *E. E. Maire*, May 1911, "plante vivace, fl. roses grandes" (holotype of *Tecoma Mairei*; photo. in A. A.).

Though this is an herbaceous species, I am including it in this enumeration, because Léveillé has described it under the ligneous genus *Tecoma*.

ACANTHACEAE

Phlogacanthus pubinervis T. Anderson in Jour. Linn. Soc. Bot. 9: 508 (1867). — Léveillé, Cat. Pl. Yun-Nan, 6 (1915).

Aeschynanthus Dunnii Léveillé in Fedde, Rep. Spec. Nov. 9: 453 (1911); Fl. Kouy-Tchéou, 180 (1914). — **Synon. nov.**

Lonicera Menelii Léveillé, Fl. Kouy-Tchéou, 63 (1914). — **Synon. nov.**

CHINA. K w e i c h o u : without precise locality, *J. Esquirol*, no. 737, "fleur rougeâtre" (syntype of *Aeschynanthus Dunnii*; photo. in A. A.); Lo-fou, *J. Cavalerie*, no. 3475, March 1909 "couleur jaunâtre" (syntype of *Aeschynanthus Dunnii*, in fruit; photo. in A. A.); Thing-mei, 1100 m., *J. Esquirol*, no. 3540, Dec. 2, 1913 (holotype of *Lonicera Menelii*; merotype in A. A.).

Cystacanthus yangtsekiangensis (Lévl.), comb. nov.

Strobilanthes yangtsekiangensis Léveillé, Cat. Pl. Yun-Nan, 7 (1915).

CHINA. Y u n n a n : rives du fleuve Bleu, alt. 400 m., *E. E. Maire*, May 1912, "plante sous-ligneuse en touffes dressées, fl. bleues" (syntype of *Strobilanthes yangtsekiangensis*, photo. in A. A.); rives du fleuve Bleu à Ta-tchai, alt. 450 m., "plante vivace, sous-ligneuse, en touffes, fl. roses" (syntype of *S. yangtsekiangensis*; photo. in A. A.).

This species is very near *C. yunnanensis* W. W. Sm., but is easily distinguished by the closer and finer pubescence of the young branchlets, the inflorescence and the calyx, and by the numerous lateral 2-6-flowered inflorescences along last year's branches. To *C. yangtsekiangensis* apparently belong Rock 8049 from Yunnan, between Tang-yueh and Likiangfu, and Schneider 671 from southern Szechuan, between Mo-so-ying and Kung-mu-ying.

RUBIACEAE

Oldenlandia Bodinieri (Lévl.) Chun in Sunyatsenia, 1: 310 (1934).

Hedyotis Bodinieri Léveillé in Fedde, Rep. Spec. Nov. 11: 64 (1912).

CHINA. K w a n g t u n g : Tay-mo-chan, sommet de la mont., 3500 ft., *E. Bodinier*, no. 1158, May 7, 1895, "petit sous-arbrisseau croissant dans les rocailles, fleurs blanches" (holotype; photo. in A. A.).

I have not been able to identify this plant with any described species.

Oldenlandia macrostemon (Hook. & Arn.) Kuntze, Rev. Gen. 1: 292 (1891). — Pitard in Lecomte, Fl. Gén. Indo-Chine, 3: 138 (1922).

Hedyotis macrostemon Hooker & Arnott, Bot. Beechey Voy. 192 (1841). — Léveillé, Cat. Pl. Yun-Nan, 245 (1917).

Hedyotis Esquirolii Léveillé in Fedde, Rep. Spec. Nov. 13: 176 (1914); Fl. Kouy-Tchéou, 367 (1915). — **Synon. nov.**

Oldenlandia Esquirolii (Lévl.) Chun in Sunyatsenia, 1: 310 (1934).

CHINA. K w e i c h o u : without precise locality, *J. Esquirol* (holotype of *H. Esquirolii*; photo. in A. A.).

Ophiorrhiza japonica Blume, Bijdr. 978 (1826).

Ophiorrhiza Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. 13: 177 (1914).

Ophiorrhiza Labordei Léveillé l. c. (1914); Fl. Kouy-Tchéou, 370 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : district de Tsin-gay, rocailles, bois à Kao-tchay, *J. Laborde* in herb. *Bodinier*, May 15, 1898 (holotype of *O. Labordei*; photo. in A. A.); without locality, *J. Cavalerie* (holotype of *O. Cavaleriei*; ex Léveillé).

Ophiorrhiza Cavaleriei is cited by Léveillé in his Flore du Kouy-Tchéou as a synonym of *O. Labordei*, but Cavalerie's specimen is not cited, only Laborde's specimen from Tsin-gay. Cavalerie's specimen I have not seen.

Ophiorrhiza cantoniensis Hance in Ann. Sci. Nat. sér. 4, 18: 222 (1862). — Léveillé, Fl. Kouy-Tchéou, 370 (1915).

Ophiorrhiza Seguii Léveillé in Fedde, Rep. Spec. Nov. 13: 177 (1914). — **Synon. nov.**

Ophiorrhiza violaceo-flammea Lévillé in Bull. Géog. Bot. 25: 47 (1915); Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. K w e i c h o u : environs de Gan-pin, croissant dans les rocailles, les trous entre des rochers, *E. Bodinier*, no. 1549, April 29, 1897, "fleurs blanches" (holotype of *O. Seguini*, photo. in A. A.). Y u n n a n : vallée de Li-tse-pin, 2700 m., *E. E. Maire*, April 1912, "sous-arbrisseau toujours vert, fl. violettes" (holotype of *O. violaceo-flammea*; photo. in A. A.).

Ophiorrhiza Seguini is not mentioned by Lévillé in his Flore du Kouy-Tchéou, but its type is enumerated, together with another specimen, under *O. cantoniensis*, which shows that Lévillé had reduced it to *O. cantoniensis*. The color of the flowers on the specimen of *O. violaceo-flammea* said to be violet does not look at all different from the color of flowers of *O. japonica*.

Ophiorrhiza cantoniensis is closely related to *O. japonica* Bl., but it may be distinguished by its oblong leaves attenuate at the base and quite glabrous, broadest at or above the middle, while *O. japonica* has shorter generally ovate or oblong leaves less attenuate or even nearly rounded at base and puberulous on the midrib beneath.

Wendlandia ligustrina Wallich, Num. List. 6272 (1832), in part, nom. nud. — Don, Gen. Syst. 2: 518 (1834). — Lévillé, Cat. Pl. Yun-Nan, 242 (1917). — Cowan in Not. Bot. Gard. Edinb. 16: 242 (1932); 18: 183 (1934).

Luculia gratissima Sw. sensu Lévillé, Fl. Kouy-Tchéou, 368 (1915), non Sweet (1826).

CHINA. K w e i c h o u : bords du Hoa-kiang, *L. Martin* in herb. *Bodinier*, no. 2563, Feb. 18, 1899, "petit arbuste, fleurs blanches" (photo. in A. A.).

This collection extends the range of *W. ligustrina* into Kweichou. Martin's specimen was identified with *W. ligustrina* by J. M. Cowan according to a note on the specimen.

Wendlandia salicifolia Franchet in herb. ex Castello in Jour. de Bot. 9: 208 (1895). — Cowan in Not. Bot. Gard. Edinb. 16: 244 (1932).

Ligustrum Thea Lévillé & Dunn in Fedde, Rep. Spec. Nov. 10: 147 (1911). — Lévillé, Fl. Kouy-Tchéou, 295 (1914).

CHINA. K w e i c h o u : without precise locality, *J. Esquirol*, no. 327, Dec. 16, 1904, "sous-arbrisseau des bords du fleuve, submergé aux grandes eaux; les feuilles donnent une infusion theiforme assez employée; fleur blanc-rose" (holotype of *Ligustrum Thea*; photo. in A. A.); without precise locality, *J. Esquirol*, no. 239 (cited in Fl. Kouy-Tchéou; photo. in A. A.).

Ligustrum Thea was first referred to *W. salicifolia* by Cowan in his "The Genus *Wendlandia*" (op. cit. 233-316).

Wendlandia Cavalieriei Léveillé in Fedde, Rep. Spec. Nov. 10: 434 (1912); Fl. Kouy-Tchéou, 373 (1915). — Cowan in Not. Bot. Gard. Edinb. 16: 263 (1932).

Wendlandia Feddei Léveillé in Fedde, Rep. Spec. Nov. 10: 434 (1912); Fl. Kouy-Tchéou, 373 (1915).

CHINA. K w e i c h o u : Lo-fou, *J. Cavalerie*, no. 3297, April 1907, "fleurs blanches" (holotype of *W. Cavalieriei*; merotype in A. A.); route de Pin-fa à Lo-fou, *J. Cavalerie*, no. 2732, April 4, 1906 (holotype of *W. Feddei*; photo. and merotype in A. A.).

Wendlandia uvariifolia Hance subsp. **Dunniana** (Lévl.) Cowan in Not. Bot. Gard. Edinb. 16: 287 (1932); 18: 185 (1934).

Wendlandia Dunniana Léveillé in Fedde, Rep. Spec. Nov. 10: 434 (1912); Fl. Kouy-Tchéou, 373 (1915).

CHINA. K w e i c h o u : Lo-fou, *J. Cavalerie*, no. 3476, March 1908 (holotype of *W. Dunniana*; merotype in A. A.).

Wendlandia longidens (Hance) Hutchinson in Sargent, Pl. Wilson. 3: 392 (1916). — Cowan in Not. Bot. Gard. Edinb. 16: 301 (1932).

CHINA. Y u n n a n : à mi-mont de Siao-ho, alt. 2800 m., *E. E. Maire*, [1911-14] "arbuste buissonnant, fl. roses" (in herb. Léveillé sub *Leptodermis Mairei*; duplicate in A. A.).

In the herbarium Léveillé there were in the cover of *Leptodermis Mairei* three specimens collected by Maire, of which two belonged to *L. Mairei* which was identified by Dr. H. Winkler as *L. pilosa* (Franch.) Diels var. *glabrescens* H. Winkl., while the third was not a *Leptodermis*, but represents the species cited above. From the Szechuan and Hupeh specimens before me it differs slightly in the smaller leaves not exceeding 14 mm. and somewhat more densely pubescent on both sides; the flowers also are slightly smaller and are rose-colored according to the collector, while Wilson under his numbers 3756 (Veitch Coll.) and 2359 gives the color of the flowers as white. Possibly the specimen cited by Cowan (l. c.) as Maire, no. 326, without locality, is of the same collection as the specimen cited above.

Emmenopterys Henryi Oliver in Hooker's Icon. 19: t. 1823 (1889).

Mussaenda Cavalieriei Léveillé in Fedde, Rep. Spec. Nov. 13: 178 (1914); Fl. Kouy-Tchéou, 368 (1915). — Hutchinson in Sargent, Pl. Wilson. 3: 397 (1916). — **Synon. nov.**

Mussaenda Mairei Léveillé in Bull. Géog. Bot. 25: 47 (1915); Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. K w e i c h o u : sur des rochers à Touan-po près Pin-yue (Pin-ue), *J. Cavalerie*, no. 2481, Aug. 10, 1905, "petit arbre à fl. blanches" (holotype of *Mussaenda Cavaleriei*; merotype in A. A.). Y u n n a n : vallée de Long-ky, 700 m., *E. E. Maire*, July 1912, "arbre moyen, fl. blanches" (holotype of *Mussaenda Mairei*; merotype in A. A.).

Adina racemosa Miquel, Cat. Mus. Bot. Lugd.-Bat. 1: 44 (Fl. Jap.) (1870).

Cornus Esquirolii Léveillé in Fedde, Rep. Spec. Nov. 13: 257 (1914); Fl. Kouy-Tchéou, 116 (1914). — **Synon. nov.**

CHINA. K w e i c h o u : rivière, Tong-tchéou, *J. Esquirol*, no. 407, June 1905 (holotype of *Cornus Esquirolii*; photo. in A. A.).

Uncaria scandens (Sm.) Hutchinson in Sargent, Pl. Wilson. 3: 406 (1916). — Léveillé, Cat. Pl. Yun-Nan, 248 (1917).

Cephalanthus Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. 10: 434 (1912); Fl. Kouy-Tchéou, 365 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : Ma-jo, *J. Cavalerie*, no. 3015, May and Nov. 1908 (holotype of *Cephalanthus Cavaleriei*; merotype in A. A.).

Besides the flowering specimen described by Léveillé there is a fruiting specimen under the same number in his herbarium which is probably the specimen collected in November. This specimen apparently represents *U. rhynchophylla* (Miq.) Miq. which is of wide distribution in Eastern Asia, but to my knowledge has not been previously collected in western China.

Neonauclea Navillei (Lévl.), comb. nov.

Cephalanthus Navillei Léveillé, Fl. Kouy-Tchéou, 365 (1915).

CHINA. K w e i c h o u : ruisseau qui monte à Kiao-miay, alt. 800 m., *J. Esquirol*, no. 3631, June 5, 1913, "arbre, 6 m." (holotype of *Cephalanthus Navillei*; merotype in A. A.).

This species is very similar to *N. Griffithii* (Hook. f.) Merr. but easily distinguished by ternate heads on a rather slender peduncle about 3 cm. long, the slender pedicels being 3–4 cm. long with scars of bractlets near the middle. The leaves are identical with those of specimens of *N. Griffithii* from Yunnan (Henry, nos. 12676 and 12880) which are in flower while Esquirol's specimen is in fruit.

Mussaenda Esquirolii Léveillé, Fl. Kouy-Tchéou, 369 (1915).

Mussaenda Wilsonii. Hutchinson in Sargent, Pl. Wilson. 3: 393 (1916). — **Synon. nov.**

CHINA. K w e i c h o u : forêts de Tong-tchéou, 1400 m., *J. Esquirol*, no. 3264, June 22, 1912 "couleur jaune pâle" (holotype of *M.*

Esquirolii; photo. in A. A.). H u p e h : Chang-lo-hsien, ravines, 650 m., *E. H. Wilson*, Arn. Arb. Exp. no. 3265, June 1907 "bracts white, flowers yellow" (holotype of *M. Wilsonii* in A. A.).

The name *Mussaenda Esquirolii* does not appear on the original specimen, but an unpublished name under another genus with the same specific epithet in L  veill  's hand. The specimen differs from the type of *M. Wilsonii* in the more conspicuous pubescence of the veins and veinlets of the under side of the leaf, but this may be due to the younger state of the leaves.

Mussaenda pubescens Aiton f., Hort. Kew ed. 2, 1: 372 (1810).

Mussaenda Bodinieri L  veill   in Bull. Soc. Bot. France, 55: 59 (1908); Cat. Pl. Yun-Nan, 246 (1917). — Hutchinson in Sargent. Pl. Wilson. 3: 396 (1916). — **Synon. nov.**

CHINA. K w a n g t u n g : pied du Tay-mo-chan (Taiman-san), commun dans les haies pr  s des villages, *E. Bodinier*, no. 1159, May 6, 1895, "arbrisseau    branches sarmenteuses, fleurs blanches; diff  rs des autres *Mussaenda* de l'absence de grande bract  e florale" (holotype of *M. Bodinieri*; photo. in A. A.).

In *Mussaenda pubescens* the enlarged calyx-lobe is sometimes much reduced in size or entirely absent. I find it entirely absent in Hongkong Herb. 2784, J. B. Norton 1475, and H. H. Chung 3391 from Fukien, and in R. C. Ching 5433 and 5435 from Kwangsi. The locality given by L  veill   as Cay-mo-chan is apparently a misprint for Tay-mo-chan as it is clearly spelled on Bodinier's label; the same locality appears on English maps as Taimau-san.

Tarenna mollissima (Hook. & Arn.) Merrill in Philipp. Jour. Sci. Bot. 13: 160 (1918). — Metcalf in Jour. Arnold Arb. 13: 29 (1932).

Ehretia Esquirolii L  veill  , Fl. Kouy-Tch  ou, 54 (1914), non L  veill   (1913).

CHINA. K w e i c h o u : route de Tong-tch  ou, 1200 m., *J. Esquirol*, no. 3775, June 1912 (holotype of *Ehretia Esquirolii* of 1914: photo. in A. A.).

The name *Ehretia Esquirolii* (in Fedde, Rep. Spec. Nov. 12: 335. 1913) had been given by L  veill   to another specimen collected by Esquirol at about the same time and at the same locality and numbered 3214. This specimen cannot be found in the L  veill   herbarium and was probably identified by L  veill   with another plant and the name used again for Esquirol 3775. The number 3775 seems to have been a mixture, for L  veill   enumerates in his Flore du Kouy-Tch  ou the same number under *Ehretia Dunniana*, *E. Esquirolii* and *E. macrophylla*; under the last named as 3775 p.p. and without locality.

Tarenna incerta Koorders & Valeton in Meded. Lands Plantent. 59: 268 (Bijdr. Boomsort. Java, 8) (1902). — Merrill in Philipp. Jour. Sci. 17: 469 (1920).

Tarenna zeylanica Koorders & Valeton, l. c. 82 (1902); non Gaertn.

? *Webera pallida* Franchet ex Brandis, Ind. Trees, 378 (1906).

Webera Cavaleriei Lévillé in Fedde, Rep. Spec. Nov. 9: 323 (1911); Fl. Kouy-Tchéou, 372 (1915).

Webera Henryi Lévillé, Sert. Yunnan. 1 (May 1916); Cat. Pl. Yunnan, 296 (1917).

Tarenna pallida (Franch.) Hutchinson in Sargent, Pl. Wilson. 3: 410 (Aug. 1916).

CHINA. K w e i c h o u : Pin-fa, *J. Cavalerie*, no. 2342, June 8, 1905, "petit arbre" (holotype of *Webera Cavaleriei*; photo. in A. A.). Y u n n a n : Szemao, *A. Henry*, no. 11923A (holotype of *Webera Henryi*; photo. in A. A.).

The type of *Webera Cavaleriei* consists only of a year-old branch with a few leaves and a small fragment of an inflorescence with very young fruits. It differs somewhat from the type of *W. Henryi* in the manifestly truncate calyx without any indication of teeth, though in the latter specimen perfectly truncate calyces occasionally occur. The type of *W. Henryi* agrees exactly with Henry no. 10686 which was identified by Hutchinson with *Tarenna pallida* together with Henry, nos. 11923, 11923c and 11923f.

Tarenna incerta seems to be somewhat variable in the number of ovules. Koorders & Valeton state that there are two or sometimes only one ovule in each locule and refer to a tree in the garden which had in all flowers only one ovule in each cell. In the one ovary of *Webera Cavaleriei* which I examined I also found only one ovule in each cell. Merrill (l. c.) states that the usual number of seeds in each fruit is apparently two. Brandis (l. c.), however, describes the fruit of *W. pallida* as having 4–6 seeds. Two fruits examined of Henry 11923f had 1 and 3 seeds each. It, therefore, seems somewhat doubtful if *Webera pallida* Franch. of which I have not seen the type really belongs to *T. incerta*.

Gardenia jasminoides Ellis in Philos. Trans. 51(2): 935, t. 25 (1761).

Gardenia florida Linnaeus, Spec. Pl. ed. 2, p. 305, 1679 (1762). —

Lévillé, Fl. Kouy-Tchéou, 366 (1915); Cat. Pl. Yunnan, 245 (1917).

Gardenia Schlechteri Lévillé in Fedde, Rep. Spec. Nov. 10: 146 (1911); Fl. Kouy-Tchéou, 366 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : without precise locality, *J. Esquirol*, no.

777, April 1905, "arbre, fl. blanche" (holotype of *G. Schlechteri*; merotype in A. A.).

Esquirol no. 777 represents a rather small-flowered form, but otherwise it does not differ from *G. jasminoides*.

Varneria augusta L. (in Amoen. Acad. 4: 136, 1759) upon which Merrill based the new combination *G. augusta*, is a nomen nudum. The oldest available specific epithet is *jasminoides*, though *florida* has been generally adopted.

Ixora Henryi Lévillé in Fedde, Rep. Spec. Nov. 13: 178 (1914); Fl. Kouy-Tchéou, 367 (1915); Cat. Pl. Yun-Nan, 245 (1917). — Pitard in Lecomte, Fl. Gén. Indo-Chine, 3: 324 (1924). — Chun in Sunyatsenia, 1: 306 (1934).

CHINA. K w e i c h o u : Lo-fou, *J. Cavalerie*, no. 3496, March 1909 (syntype; merotype in A. A.). Y u n n a n : Szemao, s. mountain forests, 5000 ft., *A. Henry*, no. 11637A, "shrub 5 ft., red flowers" (syntype; photo. and isotype in A. A.).

Here also belong Henry nos. 10407 and 10407 A-c from Mengtze and 11637 and 11637A-D from Szemao, Yunnan.

Psychotria Henryi Lévillé in Fedde, Rep. Spec. Nov. 13: 179 (1914). — Hutchinson in Sargent, Pl. Wilson. 3: 415 (1916).

CHINA. Y u n n a n : Szemao, s. e. mountains, 4000 ft., *A. Henry*, no. 12146D, "shrub 4 ft., red fruit" (holotype; photo. and isotype in A. A.).

Psychotria rubra (Lour.) Poiret, Encycl. Méth. Suppl. 4: 597 (1816).

Psychotria elliptica Ker in Bot. Reg. 8: t. 607 (1822); non H. & B. ex Roem. & Schult. (1819).

Psychotria Esquirolii Lévillé in Fedde, Rep. Spec. Nov. 10: 435 (1912); Fl. Kouy-Tchéou, 371 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : Ouang-mou, *J. Esquirol*, no. 119, June 1904 "fl. blanchâtre" (holotype of *P. Esquirolii*; photo. in A. A.).

This species has apparently not yet been recorded from western China, but seems common in southeastern China west to Kwangsi.

Psychotria Prainii Lévillé in Fedde, Rep. Spec. Nov. 9: 324 (1911); Fl. Kouy-Tchéou, 371 (1915).

CHINA. K w e i c h o u : Ouang-mou, *J. Esquirol*, 76 (holotype; photo. in A. A.); Héou-hay-tse, *J. Esquirol*, no. 860, June 1906, "fl. blanche" (enumerated in Fl. Kouy-tchéou; photo. and merotype in A. A.).

This species resembles in its capitate sessile or subsessile inflorescence *P. morindoides* Hutchins., but the inflorescence, branchlets and leaves beneath are covered with a ferrugineous pubescence similar to that of *P. pilifera* Hutchins., though shorter; besides it differs from *P. pilifera* in the sessile inflorescence, the smaller more coriaceous leaves glabrous above and in the short petioles.

Lasianthus Hookeri Clarke ex Hooker, f., Fl. Brit. Ind. 3: 184 (1880). — Léveillé, Cat. Pl. Yun-Nan, 246 (1917).

Lasianthus Dunniana Léveillé in Fedde, Rep. Spec. Nov. 11: 64 (1912); Fl. Kouy-Tchéou, 368 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : Lo-fou, *J. Cavalerie*, no. 3459, Oct. 1908 (holotype of *L. Dunniana*; photo. and merotype in A. A.).

Léveillé's description of the species is taken from a note on the type specimen which reads "aff. *L. trichophlebus* Hemsley, sed margine foliorum dense ciliata distincta," and is signed S. T. D(unn). It agrees exactly with Yunnan specimens referred by Hutchinson to *L. Hookeri* (in Sargent, Pl. Wilson. 3: 402. 1916).

Lasianthus Biermanni King ex Hooker f., Fl. Brit. Ind. 3: 190 (1880). — Léveillé, Cat. Pl. Yun-Nan, 246 (1917).

Lasianthus Esquirolii Léveillé in Fedde, Rep. Spec. Nov. 11: 295 (1912); Fl. Kouy-Tchéou, 368 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : without precise locality, *J. Esquirol*, no. 648 (holotype of *L. Esquirolii*; photo. in A. A.).

Esquirol's specimen agrees well with Henry no. 11148, identified by Hutchinson with *L. Biermanni* (in Sargent, Pl. Wilson. 3: 402. 1916).

Lasianthus Labordei (Lévl.) Rehder in Jour. Arnold Arb. 13: 340 (1932).

Canthium Labordei Léveillé in Fedde, Rep. Spec. Nov. 13: 178 (1914); Fl. Kouy-Tchéou, 384 (1915).

CHINA. K w e i c h o u : district de Tsin-gay, mont. de Kao-tchay, penchant escarpé des montagnes, *J. Laborde* in herb. *Bodinier*, no. 2109, March 7, 1898, "arbuste" (holotype of *Canthium Labordei*; photo. in A. A.).

Lasianthus Hartii Franchet in Bull. Soc. Bot. France, 46: 209 (1899).

Canthium Dunnianum Léveillé in Fedde, Rep. Spec. Nov. 9: 324 (1911); Fl. Kouy-Tchéou, 364 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : without precise locality, *J. Esquirol* (holotype of *Canthium Dunnianum*; photo. in A. A.); Pin-fa, mon-

tagnes, *J. Cavalerie*, no. 3226, May 20, 1907, "1 m. de h., fl. blanches" (cited in Fl. Kouy-Tchéou; merotype in A. A.).

In Flore du Kouy-Tchéou Léveillé cites only *Cavalerie*, no. 3226, which is in bloom, while the type, which is not cited, is a fruiting specimen.

This species is apparently related to *L. japonicus* Miq. from which it differs in the glabrous branchlets, glabrous calyx and glabrous or nearly glabrous leaves, and to *L. longicauda* Hook. f. from which it differs in the more coriaceous leaves with the veinlets less prominent beneath and in the five corolla-lobes being densely bearded inside up to the tip. The only flowering specimen of *L. longicauda* I have seen is Henry no. 10633 which has a 4-lobed corolla; this agrees with Hooker's original description of the flowers as "usually 4-merous." The flowers are also 4-merous in *Lasianthus Labordei*.

***Lasianthus* spec.**

Canthium Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. 10: 434 (1912); Fl. Kouy-Tchéou, 364 (1915).

CHINA. K w e i c h o u : Ma-jo, *J. Cavalerie*, no. 3350 (holotype of *Canthium Cavaleriei*; photo. and merotype in A. A.).

This species I am unable to identify with any species of *Lasianthus* and in the absence of flowers an exact determination is not possible. It can not be a *Canthium*, since the fruit is a several-seeded berry.

***Paederia scandens* (Lour.) Merrill** in Contr. Arnold Arb. 8: 163 (1934).

Paederia foetida Thunberg in Nov. Act. Soc. Sci. Upsal. 4: 32 (1783); Fl. Jap. 106 (1784). — Léveillé, Fl. Kouy-Tchéou, 376 (1915). — Non Linnaeus (1767).

Paederia tomentosa Blume, Bijdr. 963 (1826).

Paederia chinensis Hance in Jour. Bot. 16: 228 (1878).

Paederia Esquirolii Léveillé in Fedde, Rep. Spec. Nov. 10: 146 (1911).

Paederia Dunniana Léveillé, l. c. (1911).

Paederia Mairei Léveillé in Fedde, Rep. Spec. Nov. 13: 179 (1914).

Paederia tomentosa Bl. var. *Mairei* (Lévl.) Léveillé, Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. K w e i c h o u : Ky-che-ten, *J. Esquirol*, no. 184, Aug. 1904 (holotype of *P. Esquirolii*; photo. in A. A.); without precise locality, *J. Esquirol*, no. 775, April 1905, "fleur à gorge rouge" (holotype of *P. Dunniana*; photo. in A. A.). Y u n n a n : broussailles des collines à Siao-ou-long, 2550 m., *E. E. Maire*, July 1911, "arbuste grim-pant, odeur fétide, fl. roses" (holotype of *P. Mairei*; photo. in A. A.).

The specimens cited above represent the typical glabrous form of

P. scandens; *Paederia Esquirolii* and *P. Dunniana* have narrow generally oblong leaves cuneate at base, while *P. Mairei* has larger and broader generally ovate leaves rounded to truncate at base.

This species which is the most widely distributed of the genus has been generally called *P. tomentosa* Bl. which is described by Blume as having the leaves tomentose beneath. I have seen no specimens from the type region, but as long as I have no evidence to the contrary, I accept *P. tomentosa* Bl. as a synonym of *P. scandens*, representing the form with leaves pubescent beneath which occasionally occurs also in China.

***Paederia Wallichii* Hooker f., Fl. Brit. Ind. 3: 196 (1881).**

Paederia tomentosa Bl. var. *purpureo-caerulea* Léveillé & Vaniot in Bull. Soc. Bot. France, 55: 59 (1908).

Paederia Bodinieri Léveillé, Fl. Kouy-Tchéou, 371 (1915); non Léveillé (1914). — **Synon. nov.**

Cynanchum yunnanense Léveillé, Cat. Pl. Yun-Nan, 13 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : environs de Hoang-ko-chou, rochers, etc., *J. Seguin* in herb. *Bodinier*, no. 2501, Sept. 8, 1898, "liane grimpante, fleurs, atro-pourpre, avec bordure bleu-rouge, inodore" (holotype of *P. tomentosa* var. *purpureo-coerulea* and *P. Bodinieri*; photo. and merotype in A. A.). Y u n n a n : brousse des montagnes à Tcha-ho, alt. 2800 m., *E. E. Maire*, Nov. 1911, "arbuste grimpant, tomenteux, fl. violettes"; rives du fleuve Bleu à Siao-ho, 400 m., *E. E. Maire*, July 1912 "arbuste grimpant, feuil. blanches, velues en dessous" (syntypes of *Cynanchum yunnanense*; photos. in A. A.).

Paederia Bodinieri was described by Léveillé without reference to his earlier *P. tomentosa* var. *purpureo-caerulea*, but it is based on the same specimen which bears only the name var. *purpureo-caerulea* in Léveillé's hand. The name is a later homonym of his earlier *P. Bodinieri* (in Fedde, Rep. Spec. Nov. 13: 179. 1914) which he referred the same year to *Marlea* as *M. Cavaleriei* and which turns out to be identical with *Gardneria multiflora* Mak. (see Jour. Arnold Arb. 15: 309). *Cynanchum yunnanense* is not different from Seguin's specimen except that it has shorter inflorescences.

The specimens enumerated above are identical with Henry's nos. 9126 and 12442 and, judging from the description, seemed conspecific with *P. Wallichii* Hook. f. I am indebted to Sir Arthur W. Hill for a comparison of the Henry numbers with the type specimens of *P. Wallichii* in the Kew Herbarium; he writes me that Mr. C. E. C. Fischer reports on these specimens as follows: "the only difference between these numbers and the type of *P. Wallichii* Hook f. that I can see is that the basal

lobes of the leaves are rather more rounded and the sinus slightly deeper and also the buds rather shorter. I doubt that this would suffice for even a variety." With the material at hand *P. Wallichii* Hook. f. may be characterized by cordate to subcordate leaves densely scabrid above with setulose appressed hairs somewhat bulbous at base and densely villous-pubescent or tomentose beneath, and by the lateral branches of the inflorescence bearing one or several capitate flower clusters. In the capitate or subcapitate flowers it resembles *P. microcephala* Pierre from which it differs in the short calyx-teeth and in the dense pubescence of the leaves.

Paederia Cavaleriei Lévillé in Fedde, Rep. Spec. Nov. 13: 179 (1914).

Paederia tomentosa Bl. ex Lévillé, Fl. Kouy-Tchéou, 371 (1915). — Non Blume (1826).

CHINA. K w e i c h o u : bois des montagnes, *J. Cavalerie*, no. 2058, Aug. 1904, "plante très puante" (holotype of *P. Cavaleriei*; photo. in A. A.).

This species is similar to the preceding, but differs in the long hirsute ferrugineous pubescence of the branches, the petiole and the inflorescence, in the petiole being 7.5–8 cm. long and in the 1–1.5 mm. long fairly straight hairs thinly covering the underside of the leaves, but dense on the midrib and veins, also in the glabrous narrower calyx-teeth. According to the original description it resembles *P. pilifera* Hook. f. in the long pubescence, but Pitard (in Lecomte, Fl. Gén. Indo-Chine, 3: 412) describes the leaves as very tomentose beneath, the calyx-tube as very tomentose and the petiole as 1–2.5 cm. long.

A specimen collected in Kweichou at Sanhoa by W. Y. Chun (no. 6301) agrees in the pubescence of the stem and the leaf and in the thin texture of the leaf very well with *P. Cavaleriei*, but the lateral branches of the inflorescence end in cincinnate cymes, as is the rule in *P. scandens*, and not in subcapitate or capitate cymes, characteristic of this and the preceding species.

Leptodermis Potanini Batalin in Act. Hort. Petrop. 14: 319 (1898). — H. Winkler in Fedde, Rep. Spec. Nov. 18: 152 (1922).

Leptodermis Esquirolii Lévillé in Fedde, Rep. Spec. Nov. 9: 324 (1911); 13: 179 (1914); Fl. Kouy-Tchéou 368 (1915); Cat. Fl. Yun-Nan, 246 (1917).

CHINA. K w e i c h o u : Hin-y-fou, *J. Cavalerie*, no. 3930, July 1912 (cited in Fl. Kouy-Tchéou; duplicate in A. A.). Y u n n a n : Ouan-tse, *J. Esquirol*, no. 1503, May 22, 1909 "blanche à l'intérieur, rouge à l'extérieur" (holotype of *L. Esquirolii*; photo. in A. A.).

Léveillé published *L. Esquirolii* a second time in 1914, but with a briefer description, both based on Esquirol no. 1503 which is a flowering specimen. Cavalerie no. 3930 from Kweichou is a fruiting specimen and owing to its fully developed broader leaves looks somewhat different, but apparently belongs to this species. *Leptodermis Esquirolii* was first identified with *L. Potanini* by H. Winkler (l. c.).

Leptodermis Potanini var. **glauca** (Diels) H. Winkler in Fedde, Rep. Spec. Nov. 18: 153 (1922).

Leptodermis motsouensis Léveillé in Bull. Géog. Bot. 25: 47 (1915); Cat. Pl. Yun-Nan, 246 (1917). — **Synon. nov.**

CHINA. Y u n n a n : collines arides de Mo-tsou, 800 m., *E. E. Maire*, May 1912, "sous-arbrisseau en touffes, fl. blanches" (holotype of *L. motsouensis*; merotype in A. A.).

The identification of *L. motsouensis* with *L. Potanini* var. *glauca* was communicated to me by Dr. H. Winkler in a recent letter as were the identifications of the following species of *Leptodermis*.

Leptodermis Potanini var. **tomentosa** H. Winkler in Fedde, Rep. Spec. Nov. 18: 153 (1922).

Leptodermis tongchouanensis Léveillé in Bull. Géog. Bot. 25: 47 (1915); Cat. Pl. Yun-Nan, 246 (1917), "*tongtchouanensis*" — **Synon. nov.**

CHINA. Y u n n a n : rochers des coteaux autour de Tong-tchouan, 2550 m., *E. E. Maire*, May 1912, "arbrisseau, feuilles velues blanchâtres, fl. blanches soyeuses" (holotype of *L. tongchouanensis*; merotype in A. A.).

Leptodermis pilosa (Franch) Diels var. **glabrescens** H. Winkler in Fedde, Rep. Spec. Nov. 18: 160 (1922).

Leptodermis Mairei Léveillé in Fedde, Rep. Spec. Nov. 13: 179 (1914); Cat. Pl. Yun-Nan, 246 (1917). — **Synon. nov.**

CHINA. Y u n n a n : plaine de Long-tang, 2500 m., *E. E. Maire*, Aug. 1912, "arbuste non grimpant, en touffes, fl. violet" (holotype of *L. Mairei*; merotype in A. A.); haies, plaine de Tong-tchouan, 2500 m., *E. E. Maire*, in 1912 "arbuste buissonnant, écorce blanche, fl. roses" (in herb. Léveillé in cover of *L. Mairei*; duplicate in A. A.).

Only the specimen from Long-tang bears the name *L. Mairei* in Léveillé's hand. As Maire no. 21 Winkler (l. c.) enumerates under his *L. pilosa* var. *glabrescens* a specimen apparently of the same collection as Léveillé's type of *L. Mairei*.

Another specimen "à mi-mont de Siao-ho, 2800 m." in herb. Léveillé under *L. Mairei* belongs to *Wendlandia longidens* (Hance) Hutch. (see p 318.).

Leptodermis oblonga Bunge in Mém. Sav. Etr. Acad. Sci. St. Pétersb. 2: 108 (Enum. Pl. Chin. Bor. 34) (1833).

Leptodermis Chaneti Léveillé in Bull. Géog. Bot. 25: 47 (1915).

CHINA. H o p e i : montagnes de Ping-chan, *L. Chanet*, no. 538 bis, Aug. 1910; without precise locality, *L. Chanet*, no. 574, June 1904 (syn-types of *L. Chaneti*; merotypes in A. A.).

Prismatomeris Henryi (Lévl.), comb. nov.

Canthium Henryi Léveillé in Fedde, Rep. Spec. Nov. 13: 178 (1914); Cat. Pl. Yun-Nan, 245 (1917). — **Synon. nov.**

Prismatomeris brevipes Hutchinson in Sargent, Pl. Wilson. 3: 413 (1916). — Léveillé, Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. Y u n n a n : Meng-tse, S. E. mountains, 5000 ft., A. Henry, no. 9040F, "shrub 6 ft., fruit red" (holotype of *Canthium Henryi*; photo. in A. A.; paratype of *P. brevipes*; isotype in A. A.).

There is also an isotype of the holotype of *P. brevipes*, Henry 9040E, in the herbarium of the Arnold Arboretum and of another paratype, Henry 9040D.

CAPRIFOLIACEAE

Sambucus javanica Bl. var. **Argyi** (Lévl.), var. nov.

Sambucus Argyi Léveillé in Bull. Géog. Bot. 24(no. 3301): 292 (1914); in Mem. Acad. Ci. Arts Barcelona, ser. 3, 12: 545 (Cat. Pl. Kiang-Sou, 5) (1916).

CHINA. K i a n g s u : Ka-se-dao, trouvé venant de Tou-ka-dou, *Ch. d'Argy* [1848-66] (holotype of *S. Argyi*; photo. in A. A.); Sê-hom, (jardin), *Ch. d'Argy* [1848-66] "fruit rouge" (with *S. Argyi* in herb. Léveillé; photo. in A. A.).

This variety differs from the type in the shorter and comparatively broader more coarsely serrate leaflets, the lateral ones ovate-oblong to oblong (5×1.8), the terminal elliptic or elliptic-obovate (6×3), and slightly scaberulous on the veins.

Sambucus Argyi was first referred to *S. javanica* by H. K. Airy-Shaw according to a note on the specimens.

Viburnum erubescens Wallich, Pl. As. Rar. 2: 29, t. 143 (1830). — Léveillé, Cat. Pl. Yun-Nan, 28 (1916).

Viburnum botryoideum Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — **Synon. nov.**

CHINA. Y u n n a n : rochers, brousse de Kiao-me-ti, 3100 m., E. E. Maire, May 1913, "arbuste, fleurs roses" (holotype of *V. botryoideum*; merotype in A. A.).

Viburnum oliganthum Batalin in Act. Hort. Petrop. 13: 372 (1894).

Viburnum Stapfianum Léveillé in Fedde, Rep. Spec. Nov. 9: 443 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. K w e i c h o u : Ma-jo, *J. Cavalerie*, no. 3002, May 1908, "petit arbre, fleurs roses" (holotype of *V. Stapfianum*; merotype in A. A.).

This species seems common in Szechuan; the specimen cited above is the first I have seen from outside of that province.

Viburnum sympodiale Graebner in Bot. Jahrb. 29: 587 (1901). — Rehder in Sargent, Trees & Shrubs, 2: 83, 108, t. 139 (1908).

Viburnum Martini Léveillé in Fedde, Rep. Spec. Nov. 9: 443 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. K w e i c h o u : Pin-fa, bois, rare, *J. Cavalerie*, no. 2272, April 4, 1905, "fl. blanches" (holotype of *V. Martini*; merotype in A. A.).

Viburnum Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. 9: 442 (1911); Fl. Kouy-Tchéou, 66 (1914).

CHINA. K w e i c h o u : Pin-fa, montagnes, *J. Cavalerie*, no. 977, April 13, 1903, "h. 1 à 2 m., fl. blanches odorantes," (holotype; photo. and merotype in A. A.).

This species is closely related to *V. fallax* Graebn. and *V. chinchanense* Graebn. differing from the former in its coriaceous leaves rugulose and stellate pubescent above and from the latter in the glabrous ovaries and the leaves being sparingly stellate-pubescent and somewhat scabrid above. Both related species have been collected in Kweichou; *V. fallax* is represented in this herbarium from Kweichou by Steward, Chiao & Cheo 11, and *V. chinchanense* by Y. Tsiang 7419 and 9216 and also by another specimen, Tsiang 8424, which approaches *V. Rosthornii* Graebn. by its larger subcordate leaves sparingly stellate above.

Viburnum congestum Rehder in Sargent, Trees & Shrubs, 2: 111 (1907). — Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — P'ei in Mem. Sci. Soc. China 1 (no. 3): 90 (Verben. China) (1932).

Hedyotis Mairei Léveillé in Fedde, Rep. Spec. Nov. 13: 176 (1914); Cat. Pl. Yun-Nan, 245 (1917). — **Synon. nov.**

Viburnum Mairei Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — **Synon. nov.**

Premna Esquirolii Léveillé, Sert. Yunnan. 3 (1916); Cat. Pl. Yun-Nan, 298 (1917).

Oldenlandia Mairei (Lévl.) Chun in Sunyatsenia, 1: 314 (1934).

CHINA. Y u n n a n : brousse du plateau de Ta-hai-tse, alt. 3200 m., *E. E. Maire*, May (1912 or 1913), "grande arbuste, feuilles caduques, fl. blanches" (holotype of *Hedyotis Mairei*, named *H. yunnanensis*

on the label of the type specimen; photo. in A. A.); brousse au pied de Io-chan, 3200 m., *E. E. Maire*, May 1912, "arbuste haut 1.30 m.," (holotype of *V. Mairei*; merotype in A. A.); brousse des montagnes à Motsou, 800 m., *E. E. Maire*, May 1912, "arbuste, feuilles caduques, fl. blanches" (holotype of *Premna Esquirolii*; merotype in A. A.).

The three specimens cited above have the corolla tube somewhat shorter than in the type of *V. congestum*, the tube being only slightly longer than the lobes, but in the otherwise similar *V. utile* Hemsl. the tube is wide-campanulate and much shorter than the lobes. *Viburnum congestum* differs from *V. utile* also in the less dense grayish tomentum of the under side of the leaves, the individual hairs being distinguishable and usually have shorter rays, while in *V. utile* they are matted and the tomentum is whitish, brownish on the veins in young leaves. There are, however, specimens of *V. congestum* with a denser tomentum similar to that of *V. utile*. Geographically the two species seem to be well separated; *V. congestum* is common in Yunnan and extends into Kweichou and western Szechuan, while *V. utile* occurs in Hupeh and extends to eastern Szechuan.

***Viburnum cylindricum* Ham. var. *crassifolium* (Rehd.) Schneider** in Bot. Gaz. 64: 77 (1917).

Viburnum crassifolium, Rehder in Sargent, Trees & Shrubs, 2: 112 (1908).—Léveillé, Cat. Pl. Yun-Nan, 28 (1915).

Viburnum pinfaense Léveillé in Fedde, Rep. Spec. Nov. 9: 442 (1911); pro parte, quoad Cavalerie no. 1483; Fl. Kouy-Tchéou, 66 (1914).—**Synon. nov.**

CHINA. Kweichou: Pin-fa, bois, *J. Cavalerie*, no. 1483, Oct. 12, 1903 (syntype of *V. pinfaense*; merotype in A. A.).

This variety has been collected in Kweichou in three different localities by Y. Tsiang (nos. 4121, 7558 and 9137). The leaves of Cavalerie's specimen are unusually small and narrow.

Under *V. pinfaense* Léveillé describes two different plants, of which the fruiting specimen belongs here, while the flowering one belongs to *V. sempervirens* K. Koch.

***Viburnum ternatum* Rehder** in Sargent, Trees & Shrubs, 2: 37, 112 t. 117 (1907).

Viburnum Chaffanjonii Léveillé in Fedde, Rep. Spec. Nov. 9: 443 (1911); Fl. Kouy-Tchéou, 66 (1914).—**Synon. nov.**

CHINA. Kweichou: Pin-fa, bois presque à pic, *J. Cavalerie*, no. 3093, July 2, 1907 (holotype of *V. Chaffanjonii*; merotype in A. A.).

This very distinct species, differing in its ternate leaves from all other species, was known to me before only from Szechuan: banks of Min

River (Wilson 3736), Mt. Omei (W. P. Fang 2461, 2631, 3309, 3355 and F. T. Wang 23138), and Kuan-hsien (W. P. Fang 2021).

Viburnum Schneiderianum Handel-Mazzetti in Akad. Wiss. Wien Anzeig. 1925: 66 (Pl. Nov. Sin. Forts. 33: 4) (1925).

CHINA. Y u n n a n : rochers de Io-chan, alt. 3200 m., *E. E. Maire*, May (1911-13), "arbrisseau rampant, toujours vert," (in herb. Léveillé sub *Gaultheria crenulata*; duplicate in A. A.).

The specimen cited above was referred by Léveillé to *Gaultheria crenulata* Kurz and represents, at least partly, the plant enumerated under that name in his Cat. Pl. Yun-Nan, 86 (1916).

Viburnum sempervirens K. Koch, Hort. Dendr. 300 (1853). — Rehder in Sargent, Trees & Shrubs, 2: 95, 113, t. 145 (1908).

Viburnum pinfaense Léveillé in Fedde, Rep. Spec. Nov. 9: 442 (1911), pro parte, quoad specim. no. 1056; Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. K w e i c h o u : Pin-fa, montagnes, *J. Cavalerie*, no. 1056, June 11, 1903 (syntype of *V. pinfaense*; merotype in A. A.).

This species seems to be rare in western China. I have seen it only from Pin-fa, Kweichou (Cavalerie 1056 and Y. Tsiang 6385), and from Szemao, Yunnan (Henry 12753).

Viburnum foetidum Wallich, Pl. As. Rar. 1: 49, t. 61 (1830). — Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — P'ei in Mem. Sci. Soc. China, 1, no. 3: 90 (Verben. China) (1932).

Viburnum ajugifolium Léveillé in Fedde, Rep. Spec. Nov. 9: 441 (1911); Fl. Kouy-Tchéou, 65 (1914). — **Synon. nov.**

Premna Valbrayi Léveillé, Sert. Yunnan. 4 (1916); Cat. Pl. Yun-Nan, 299 (1917).

CHINA. K w e i c h o u : environs de Kouy-yang, mont du Collège, c. dans les haies, bords des ruisseaux, *E. Bodinier*, no. 2231, May 18, 1898, "fl. blanches" (holotype of *V. ajugifolium*; merotype in A. A.). Y u n n a n : haies et brousses des montagnes, à Tong-tchouan, 2500-2700 m., *E. E. Maire*, July 1912, "arbuste grêle, feuill. caduques" (holotype of *Premna Valbrayi*; merotype in A. A.).

The two specimens cited above are similar to the form described as *V. ceanothoides* C. H. Wright.

Viburnum foetidum var. **rectangulatum** (Graebn.) Rehder in Sargent, Trees & Shrubs, 2: 114 (1908), "*rectangulum*."

Viburnum Touchanense Léveillé in Fedde, Rep. Spec. Nov. 9: 442 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

Hedyotis yunnanensis Léveillé in Fedde, Rep. Spec. Nov. 13: 176 (1914); Cat. Pl. Yun-Nan, 245 (1917). — **Synon. nov.**

Oldenlandia yunnanensis (Lévl.) Chun in Sunyatsenia, 1: 310 (1934).

CHINA. K w e i c h o u : environs de Tou-chan, bord de la route, *J. Cavalerie*, no. 2192, July 5, 1897, "arbrisseau aux fleurs odorantes" (holotype of *V. Touchanense*; merotype in A. A.). Y u n n a n : broussailles des collines à Long-ky, alt. 700 m., *E. E. Maire*, June 1911, "arbuste à feuilles caduques, fl. blanches" (holotype of *Hedyotis yunnanensis*; photo. in A. A.).

Viburnum setigerum Hance in Jour. Bot. 20: 261 (1882). — Rehder in Jour. Arnold Arb. 12: 77 (1931).

Viburnum theiferum Rehder in Sargent, Trees & Shrubs, 2: 45, 113, t. 121 (1907).

Viburnum Bodinieri Léveillé in Fedde, Rep. Spec. Nov. 9: 442 (1911); Fl. Kouy-Tchéou, 65 (1914).

CHINA. K w e i c h o u : environs de Kouy-yang, bois de Kin-lin-chan, *E. Bodinier*, no. 2193, April 14, 1898, "arbuste, fl. blanches" (syntype of *V. Bodinieri*; merotype in A. A.); Pin-fa, bois ombreux, *J. Cavalerie*, no. 1285, May, 1903, "fl. blanches, odorantes" (syntype of *V. Bodinieri*; photo. in A. A.).

Viburnum Bodinieri was identified with *V. setigerum* by the writer and the identification published in 1931 (l. c.). The species has been collected in Kweichou also by Y. Tsiang near Tsunyi (no. 5318) and on the Yun-fu-shan near Pin-fa (no. 5510) and near Tuyun (5942).

Viburnum corylifolium Hooker f. & Thomson in Jour. Linn. Soc. 2: 174 (1858).

Viburnum Dunnianum Léveillé in Fedde, Rep. Spec. Nov. 9: 442 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

Viburnum barbigerum Léveillé, Fl. Kouy-Tchéou, 65 (1914). — **Synon. nov.**

CHINA. K w e i c h o u : route de Pin-yue à Kouy-yang, bords d'une rivière, *L. Martin* in herb. *Bodinier*, no. 2598, May 13, 1899, "grand arbuste, fl. blanches"; environs de Kouy-yang, mont du Collège, *J. Chaffanjon*, May 1, 1898, "arbuste, fl. blanches"; route de Pin-fa à Oug-lan, *J. Cavalerie*, Aug. 1908 "fruite rouge" (syntypes of *V. Dunnianum*; photos. of Martin's and Cavalerie's specimens, merotype of Chaffanjon's specimen in A. A.); Pin-fa, bois de hautes montagnes, *J. Cavalerie*, no. 1742, Aug. 1904 (holotype of *V. barbigerum*; merotype in A. A.).

Viburnum barbigerum agrees in all its characters with the other specimens cited, but the fruits are strikingly different in being densely covered with long setose hairs. I suspect, however, that this development

of hairs is abnormal, since I have found a few other specimens of *Viburnum* namely R. C. Ching nos. 2826 and 2952 of *V. ichangense* (Hemsl.) Rehd. from Anhwei with some of the fruits densely covered with similar, though somewhat shorter, hairs, while the rest of the fruits was perfectly normal and glabrous.

Viburnum corylifolium is perhaps only a variety of *V. dilatatum* Thbg. differing chiefly in the long spreading hairs of the young branchlets, inflorescence and petioles, while in *V. dilatatum* these parts are covered by a short and close stellate tomentum. *Viburnum corylifolium* has been collected in Kweichow also by Y. Tsiang (no. 5779) near Tu-yun and by Steward, Chiao and Cheo, (no. 583) on Niu-tu-shan; *V. dilatatum* was collected by Y. Tsiang (no. 6270) on Yao-ren-shan, Sanhoa.

***Viburnum erosum* Thbg. var. *Taquetii* (Lévl.) Rehder** in Sargent, Pl. Wilson. 1: 311 (1912). — Nakai in Nakai & Koidzumi, Trees & Shrubs Jap. ed. 2, 1: 609 (1927). — Makino & Nemoto, Fl. Jap. ed. 2, p. 1146 (1931).

Viburnum Taquetii Léveillé in Fedde, Rep. Spec. Nov. 9: 443 (1911).

Viburnum erosum var. *punctatum* Franchet & Savatier ex Nakai, Fl. Sylv. Kor. 11: 42, t. 12 c. d (1921) quoad synonym. *V. Taquetii* Lévl., vix Franch. & Sav.

CHINA. K o r e a : Quelpaert, in silvis Yengsil, 1000 m., *E. Taquet*, no. 4281, Aug. 12, 1910 (holotype of *V. Taquetii*; photo. and isotype in A. A.).

This peculiar variety chiefly characterized by the narrow leaves partly with two basal lobes near the base has been collected in Quelpaert also by E. H. Wilson (no. 9406). Nakai in 1921 (l. c.) referred it to *V. erosum* var. *punctatum* Franch. & Sav., but that variety represents apparently the plant with broader leaves densely stellate-pubescent above which seems to be the most widely distributed form. The glabrous or glabrescent form, var. *laeve* Franch. & Sav., which seems much rarer must be considered the typical form, since Thunberg (Fl. Jap. 124) describes the leaves as glabrous.

***Dipelta yunnanensis* Franchet** in Rev. Hort. 1891: 246, fig. 62. — Léveillé, Cat. Pl. Yunnan, 27 (1915).

Cavaleriella Dunniana Léveillé, Fl. Kouy-Tchéou, 61 (1914). —

Synon. nov.

CHINA. K w e i c h o u : hautes montagnes, Long-ly, *J. Cavalerie*, no. 3023, May 1908 (holotype of *Cavaleriella Dunniana*; merotype in A. A.).

The leaves are pilose on the midrib and veins beneath, also the young branchlets and the inflorescence are pilose.

Abelia verticillata Léveillé, Fl. Kouy-Tchéou, 61 (1914).

CHINA. K w e i c h o u : Pin-fa, ruisseau du sud, *J. Cavalerie*, no. 497, Sept. 1912, "fl. blanche-violette-pourprée" (holotype; photo. in A. A.).

This species appears to be closely related to *A. uniflora* R. Br. and *A. Graebneriana* Rehd., but differs from both in the pilose branches and in the ovary being pilose with rather long white hairs; it also differs from the former in the ciliate leaves and from the latter in the subcoriaceous leaves not bearded in the axils and without hairs alongside the midrib and the base of the lateral veins. On one of the branches of the type specimen the leaves are in whorls of threes, from which the specific epithet is derived, but the other branch has opposite leaves; branches with ternate leaves are also occasionally found in *A. uniflora* and in other species, e. g. in Wilson no. 747 of *A. parvifolia* Hemsl.

Abelia Schumannii (Graebn.) Rehder in Sargent, Pl. Wilson. 1: 121 (1911). — Léveillé, Cat. Pl. Yun-Nan, 26 (1915).

Strobilanthesis deutziaefolius Léveillé in Fedde, Rep. Spec. Nov. 12: 20 (1913).

Abelia deutziaefolia (Lévl.) Léveillé, Fl. Kouy-Tchéou, 60 (1914). —

Synon. nov.

Strobilanthes deutziaefolia, Léveillé, l. c. (1914), pro synonym.

Abeliae deutziaefoliae. — Ind. Kew. Suppl. 4: 252 (1921).

Abelia Mairei Léveillé, Cat. Pl. Yun-Nan, 26 (1915). — **Synon. nov.**

CHINA. K w e i c h o u : sous bois, *J. Esquirol*, no. 466, June 1905, "sous-arbrisseau, fl. blanches, panachées de rose," (holotype of *Strobilanthesis deutziaefolius*; merotype in A. A.). Y u n n a n : rochers des collines à Siao-ou-long, 2250 m., *E. E. Maire*, June 1912, "arbuste délicat, buissonnant, haut 0.80 m., fl. roses (holotype of *A. Mairei*; merotype in A. A.).

The leaves of Esquirol's no. 466 are rather large being up to 3.5 cm. long and resemble somewhat those of *A. Graebneriana* Rehd., though scarcely acuminate, but the branchlets are pubescent.

Abelia myrtilloides Rehder in Sargent, Pl. Wilson. 1: 120 (1911).

Strobilanthesis hypericifolius Léveillé in Fedde, Rep. Spec. Nov. 12: 20 (1913), "*hypericifolia*."

Abelia Bodinieri Léveillé, Fl. Kouy-Tchéou, 61 (1914) pro synonym.

A. parvifoliae.

Abelia parvifolia Hemsl. sec. Léveillé, Fl. Kouy-Tchéou, 61 (1914), saltem quoad specim. Bodinier, no. 1607, vix Hemsley.

Strobilanthes hypericifolia Léveillé, l. c. (1914), pro synonym. *A. parvifoliae*. — Ind. Kew. Suppl. 5: 252 (1921).

CHINA. K w e i c h o u : mont de Lou-tsong-koan, 1500 m., Kien-

lin-shan ça at là dans les montagnes rocailleuses, *E. Bodinier*, no. 1607, June 1, 1897 and June 19, 1899, "petit arbuste à jolies fleurs roses" (syntypes of *Strobilanthes hypericifolius*; photo. and merotype in A. A.).

Léveillé cites in his Flore du Kouy-Tchéou (l. c.) under *A. parvifolia* as synonyms besides *Strobilanthes hypericifolia* the unpublished name *A. Bodinieri*; both names appear on the labels of the type sheet of Bodinier no. 1607. The two specimens on the type sheet are somewhat intermediate between *A. myrtilloides* and *A. parvifolia* Hemsl., but in the oblong-elliptic or oblong-ovate shape of the leaves glabrous above and nearly so beneath they seem closer to the former, only in the glandular under surface they approach *A. parvifolia* which typically has ovate leaves of thicker texture pilose and glandular on both surfaces. A form very similar to Bodinier's specimen was collected near Kwei-yang, Kweichou, by Handel-Mazzetti, (no. 10477) who determined it as "*A. parvifolia* Hemsl. trans. ad *A. myrtilloides* Rehd."

Abelia Cavaleriei Léveillé, Fl. Kouy-Tchéou, 60 (1914).

CHINA. K w e i c h o u : sud de Tin-fan, mont. rocheuses, *J. Cavalerie*, no. 1909, Oct. 1904, "fl. blanches" (holotype; merotype in A. A.).

This is a very distinct species on account of its subcoriaceous leaves which recall those of *Ligustrum strongylophyllum* Hemsl. The species is apparently nearest *A. chinensis* R. Br., but is readily distinguished by the subcoriaceous perfectly glabrous quite entire leaves broadly ovate to orbicular-ovate, 1-2 cm. long, rounded or broadly cuneate at base, obtuse or rounded and apiculate at the apex. The branchlets and the many flowered terminal inflorescence are minutely puberulous. The specimen is in fruit but according to the collector the flowers are white.

Lonicera tangutica Maximowicz in Bull. Acad. Sci. St. Pétersb. 24: 48 (1877); in Mél. Biol. 10: 75 (1877).

Lonicera Rocheri Léveillé in Bull. Géog. Bot. 24(no. 301): 289 (1914); Cat. Pl. Yun-Nan, 27 (1915). — **Synon. nov.**

CHINA. Y u n n a n : brousse de Lan-mou-kiao, 3000 m., *E. E. Maire*, May 1912, "arbuste en touffes; fl. jaunes" (holotype of *L. Rocheri*; merotype in A. A.).

The species cited above differs somewhat from typical *L. tangutica* in the linear-lanceolate somewhat leafy bracts about twice as long as ovary, in the anthers being exerted about one-half and in the less slender corolla-tube, but in its other characters it agrees with this species.

Lonicera ligustrina Wallich in Roxburgh, Fl. Ind. ed. 2, 2: 179 (1824). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera missionis Léveillé, Fl. Kouy-Tchéou, 63 (1914), pro parte, quoad specim. "Esquirol (May 10, 1906), Chaffanjon no. 2215"; Cat. Pl. Yun-Nan, 27 (1915).

CHINA. K w e i c h o u : environs de Kouy-yang, mont. du Collège, à la cascade, *J. Chaffanjon* in herb. *Bodinier*, no. 2215, April 14, 1898, "arbuste" (syntype of *L. missionis*; photo. in A. A.); mont du Collège, grotte, *J. Esquirol*, May 10, 1906 "fl. blanches" (syntype of *L. missionis*; merotype in A. A.). Y u n n a n : sous bois de couteaux à Long-ky, 700 m., *E. E. Maire*, "arbuste toujours vert, fl. blanches," (in herb. Léveillé under *L. missionis*; duplicate in A. A.).

This species has been collected in Kweichou also by W. Tsiang (nos. 4580, 5972, 7640) and by Steward, Chiao & Cheo (no. 244).

Lonicera pileata Oliver in Hooker, Icon. Pl. 16: t. 1585 (1887). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera missionis Léveillé, Fl. Kouy-Tchéou, 63 (1914) pro parte, quoad specimen "Laborde 2502"; Cat. Pl. Yun-Nan, 27 (1915). —

Synon. nov.

Lonicera buxifolia Léveillé, Fl. Kouy-Tchéou, 63 (1914); Cat. Ill. Seu-Tchouen, t. 11 (1918) MS. — **Synon. nov.**

CHINA. K w e i c h o u : environs de Tsin-gay à Kia-la-tchong, *J. Laborde* in herb. *Bodinier*, no. 2502, Nov. 1898 "les fruits sont des jolies perles bleu-tendre, pulpeuses" (syntype of *L. missionis*; photo. in A. A.); environs de Kouy-yang, mont du Collège, rochers de la cascade, au bords de l'eau, *J. Chaffanjon* in herb. *Bodinier*, no. 2169, April 12, 1898, "fl. jaunâtres" (syntype of *L. buxifolia*; photo. in A. A.); grotte du Collège, 1350 m., *J. Esquirol*, no. 2069, April 1910, "blanche" (syntype of *L. buxifolia*; photo. in A. A.); Pin-fa, ruisseaux, *J. Cavalerie*, no. 1319, April 9, 1902, "fl. blanche" (in herb. Léveillé under *L. buxifolia*; photo. in A. A.).

This species has been collected in Kweichou also by Y. Tsiang (nos. 4529, 4562, 7937) and by Steward, Chiao & Cheo (no. 803); the last named specimen is approaching in the shape of its leaves f. *linearis* Rehd. The specimens named *L. buxifolia* by Léveillé differ from typical *L. pileata* in their rather small leaves. The two species, *L. ligustrina* and *L. pileata*, are closely related and connected by intermediate forms in regard to shape of the corolla and of the leaves and to pubescence. Without flowers *L. ligustrina* may be distinguished by the leaves being generally ovate, rounded at base, acuminate, and with the midrib more or less impressed above at least toward the base and strigose, while *L. pileata* has generally elliptic to oblong leaves, narrowed at base, obtuse to acute at apex, with the midrib distinctly elevated above and glabrous. In regard to shape and pubescence of the leaves *L. nitida* Wils. seems

intermediate between the two, but the leaves are much smaller and usually broader, generally ovate, but not acuminate. *Lonicera virgultorum* W. W. Sm. is very close to *L. ligustrina* and chiefly distinguished by the shape of the corolla.

Lonicera fragilis Léveillé in Fedde, Rep. Spec. Nov. 13: 337 (1914); Cat. Pl. Yun-Nan, 37 (1915).

CHINA. Y u n n a n : vallée de Li-tse-pin, 2800 m., E. E. Maire, April 1913, "arbuste cassant, haut de 1.20 m., fl. roses" (holotype; merotype in A. A.).

Frutex metralis ramis hornotinis sparse setosis vel glabris; gemma terminalis interdum evoluta perulis duabus exterioribus et 4-6 interioribus. Folia nondum plane evoluta, elliptico-oblonga, acuminata, basi cuneata, utrinque hirsuta, glandulis sparsis intermixtis, margine ciliata et stipitato-glandulosa. Flores praecoces in axillis bractearum ad basin ramulorum; pedunculi brevissimi glabri; bracteae late ovatae, 8-10 mm. longae, irregulariter eroso-denticulatae, basin versus ciliatae et sparsissime stipitato-glandulosae, apicem versus glabrae, ceterum extus intusque glaberrimae; ovaria subglobosa, glabra; calyx ovario circiter duplo longior, latus et plicatus, dentibus carnosulis inaequalibus 1.5-3 mm. longis, late ovatis apice rotundatis margine irregulariter erosulis glabris; corolla rosea (ex collectore), infundibuliformis, tubo 7-8 mm. longo basi manifeste gibboso supra paullo ampliato extus basi excepta sparse setoso-hirsuta, intus a medio ad faucem villosulo-hirsuto, lobis late ovatis apice rotundatis 3 mm. longis glabris; stamina medio tubo affixa, antheris 2.5 mm. longis faucem non attingentibus, filamentis glabris brevissimis; stylus medium tubum non superans, glaber.

As Léveillé's description is very brief and inaccurate particularly in regard to the calyx which he describes "calyce ciliato," apparently taking the bracts for the calyx, I have given above a more complete description. The species seems nearest to *L. nubigena* Rehd., from which it chiefly differs in the bracts being quite glabrous except ciliate toward the base, in the large calyx, in the corolla being sparingly setose-hirsute outside, not short-pubescent and glandular, in the hirsute pubescence at the mouth with the anthers much below the mouth, not just reaching the mouth as in *L. nubigena*, and in the glabrous style.

Lonicera lanceolata Wallich in Roxburgh, Fl. Ind. ed. 2, 2: 177 (1824). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera acrophila Léveillé in Bull. Géog. Bot. 24(no. 301): 289 (1914); Cat. Pl. Yun-Nan, 27 (1915). — **Synon. nov.**

CHINA. Y u n n a n : haut plateau de Je-ma-tchouan, 3200 m.,

E. E. Maire, July 1912, "arbre moyen, fl. roses" (holotype of *L. acrophila*; merotype in A. A.).

According to *Maire* this is a medium-sized tree, but by most collectors it is described as a shrub, 4–8 ft. tall.

Lonicera Koehneana Rehder in Sargent, *Trees & Shrubs*, 1: 41, t. 21 (1902). — *Léveillé*, *Cat. Pl. Yun-Nan*, 27 (1915).

Lonicera gynopogon *Léveillé* in *Bull. Géog. Bot.* 24 (no. 301): 289 (1914); *Cat. Pl. Yun-Nan*, 27 (1915). — **Synon. nov.**

CHINA. Y u n n a n : brousse derrière Tong-tchouan, alt. 2550 m., *E. E. Maire*, May 1912, "*Lonicera* non grimpant, rameaux courts et grêles, fl. blanc-jaune" (holotype of *L. gynopogon*; photo. in A. A.); haies, plaine de Tong-tchouan, alt. 2500 m., *E. E. Maire*, May [1912], "fl. de *Lonicera*, mi-blanche, mi-jaune" (in herb. *Léveillé* under *L. gynopogon*; photo in A. A.); haies de Tchéou-kia-tse-tang, alt. 2500 m., *E. E. Maire*, "arbuste buissonnante, haut 2 m., feuilles molles, velues et blanches en dessous, fl. mi-blanches, mi-jaunes, inodores" (in herb. *Léveillé* under *L. gynopogon*; duplicate in A. A.).

Specimens from the same locality and partly apparently of the same collection have been distributed by the Arnold Arboretum under *Maire*, no. 142 and no. 286.

Lonicera Pampaninii *Léveillé* in *Fedde, Rep. Spec. Nov.* 10: 145 (1911); *Fl. Kouy-Tchéou*, 64 (1914); *Cat. Pl. Yun-Nan*, 27 (1915).

Lonicera Henryi var. *setuligera* W. W. Smith in *Not. Bot. Gard. Edinb.* 10: 47 (1917).

CHINA. K w e i c h o u : mont de Lou-tsong-koan, Tsin-gay, rocaillies à Ché-tiou-tchay, Gan-pin, buissons et rochers de la montagne, *L. Martin* in herb. *Bodinier*, no. 1623, June 10, 1897 and June 27, 1899, "fleurs jaunes" (syntypes; merotype in A. A.).

This species is similar to *L. Henryi* Hemsl., but is easily distinguished by the slenderer corolla-tube densely clothed with reflexed yellowish hairs; in the subsessile or sessile flowers with subulate pilose bracts exceeding the pilose calyx-lobes; the leaves which closely resemble those of *L. Henryi* are pilose on the midrib above and below otherwise glabrous even on the margin.

This species has been collected in Kweichou also by Y. Tsiang near Tsun-yi and Pin-fa; nos. 5277 and 5377; also Steward, Chiao & Cheo no. 271 from Tsun-yi is probably the same, but it has no flowers.

Lonicera macrantha Sprengel, *Syst. Veg.* 4²: 82 (1827). — *Léveillé*, *Fl. Kouy-Tchéou*, 63 (1915).

Lonicera Guillonii *Léveillé* & Vaniot, in *Bull. Soc. Bot. France*, 51: cxliv (1904).

CHINA. K w e i c h o u : Pin-fa, *J. Cavalerie*, no. 1015, May 28, 1903, "fl. blanches et jaunes au vieillissant, sans odeur" (holotype of *L. Guilloni*; photo. in A. A.).

Cavalerie no. 1015 is cited by Lévillé in his *Flore du Kouy-Tchéou* under *L. macrantha* (l. c.), but the name *L. Guilloni* is not mentioned. The specimen differs somewhat from typical *L. macrantha* in the shorter and slighter pubescence of the branches and in the scarcely ciliate leaves.

Lonicera Esquirolii Lévillé, *Fl. Kouy-Tchéou*, 63 (1914).

CHINA. K w e i c h o u : without locality, *J. Esquirol*, no. 889, June 1903, "fl. jaunes après floraison" (holotype; photo. and merotype in A. A.).

This species seems most nearly related to *L. ferruginea* Rehd., but is easily distinguished by the shorter, not hirsute pubescence and the glabrous ovary. From *L. inodora* W. W. Sm. it differs in the glabrous style, the glandular pubescence of the corolla, the sessile or subsessile inflorescence and in the setulose pubescence extending over the whole under surface of the leaf.

Lonicera japonica Thunberg, *Fl. Jap.* 89 (1784). — Lévillé, *Cat. Pl. Yun-Nan*, 27 (1915); in *Mem. Acad. Ci. Art. Barcelona*, ser. 3, 12: 545 (*Cat. Pl. Kiang-Sou*, 5) (1916).

Lonicera Fauriei Lévillé & Vaniot in *Fedde, Rep. Spec. Nov.* 5: 100 (1908). — **Synon. nov.**

JAPAN. N i p p o n : in littore Shiogama, *U. Faurie*, no. 6823, Oct. 1905 (holotype of *L. Fauriei*; photo. and merotype in A. A.).

Lévillé compares his species with *L. bracteolaris* Boiss. & Buhse and describes the fruit as having 3 persistent hairy styles; he apparently mistook for styles the sepals which in one of the fruits appear to be only three, the other two not being clearly visible.

Lonicera yunnanensis Franchet in *Jour. de Bot.* 10: 310 (1896).

Lonicera Mairei Lévillé in *Bull. Bot. Géog.* 24: 289 (1914). — **Synon. nov.**

CHINA. Y u n n a n : collines herbeuses autour de Tong-tchouan, alt. 2550 m., *E. E. Maire*, fl. blanc-jaunâtre" (holotype of *L. Mairei*; merotype in A. A.).

The branches of Maire's specimen are apparently from different plants; one has the leaves quite glabrous beneath as in the type of *L. yunnanensis*, while in the other they are slightly pubescent beneath and are referable to var. *tenuis* Rehd., but there is no difference in the size of the leaves.

COMPOSITAE

Pertya Bodinieri Vaniot in Bull. Acad. Intern. Géog. Bot. **12**: 116 (1903). — Beauverd in Bull. Soc. Bot. Genève, sér. 2, **1**: 386, fig. 6 (1909). — Lévillé, Cat. Pl. Yun-Nan, 47 (1915).

CHINA. Y u n n a n : environs de Yunnan-fou, dans les ravines de la montagne, *E. Bodinier*, no. 10, Jan. 27, 1897, "tiges sous-ligneuses, de 0.6–1 m., fl. roses" (holotype; merotype [from herb. Lévillé] and photo. of isotype [in herb. Paris] in A. A.).

Though this is not one of Lévillé's species I have included it here, since the type is in the herb. Lévillé.

Pertya Esquirolii Lévillé (in Bull. Géog. Bot. **24**: 251 (1914); Fl. Kouy-Tchéou, 100 (1914) from Kweichou, based on Esquirol no. 3633 is an herbaceous plant and belongs to *Ainslea*; it seems very near or identical with *A. rubrifolia* Franch. which I have not seen.

(To be continued)

HERBARIUM, ARNOLD ARBORETUM,

HARVARD UNIVERSITY.

HUODENDRON, A NEW GENUS OF STYRACACEAE

ALFRED REHDER

*With plates 151 and 152 and one text figure.***Huodendron**, gen. nov.

Flores hermaphroditi, actinomorphi, pentameri; calycis tubus ovario adnatus, dentibus 5 triangularibus vel ovatis circiter dimidium tubum aequantibus; petala 5, initio basi coherentia, demum libera, lineari-oblonga, anguste imbricata vel valvata, sub anthesi revoluta; stamina 7–10, uniserialia, libera, petalis subaequilonga, sed ob petala revoluta valde exserta, filamentis complanatis linearibus, antheris anguste oblongis introrsis, loculis distinctis, connectivo cum filamento continuo et supra antheras in appendicem conspicuum tri- vel rarius bidentatum elongato; ovarium inferum, triloculare; styli 3, triente inferiore vel fere ad apicem connati, stigmatibus capitellatis; ovula in quoque loculo numerosa, axi centrali affixa, erecta. Fructus capsularis, ovoideus, parva, triente infra apicem sepalis circumcincta, trilocularis, loculicide dehiscens, valvis interdum demum septicidis, endocarpio crustaceo, exocarpio tenui; semina numerosa, scobiformia, minuta, oblonga vel elliptico-oblonga, leviter complanata, testa tenui reticulata, basi et apice fimbriata et saepius ad marginem sparse breviterque fimbriata, albuminosa, embryo centralis, rectus. — Arbor vel frutex ramis gracilibus, gemmis parvis nudis pubescentibus; folia decidua, alterna, petiolata estipulata, ovato-elliptica vel ovato-oblonga, acuminata, basi cuneata, integra vel remote minuteque denticulata, glabra vel fere glabra, penninervia, nervis curvatis anastomosantibus; inflorescentiae terminales et axillares, paniculatae vel subcorymbosae, ebracteatae et ebracteolatae, floribus satis parvis albis graciliter pedicellatis; capsula parva, pedicello recurvo.

Ab aliis Styracacearum generibus, petiolis et staminibus liberis vel fere liberis, filamentis supra antheram in appendicem 3-vel 2-dentatum elongatis, stylo 3-fido, capsula valvis 3 dehiscente, seminibus scobiformibus numerosis bene distincta. Ob semina numerosa *Alniphylo* affinis videtur, sed petalis et staminibus liberis, stylo trifido, connectiva appendiculato, capsula 3-loculari subinfera, seminibus scobiformibus circiter 1 mm. longis facile distinguitur.

TYPE SPECIES: *Huodendron tibeticum* (Anthony) Rehd.

DISTRIBUTION: The genus is restricted to southern China and extends

northwest across the border into southeastern Tibet and northeastern Burma and south into northern Tonkin, where it occurs near Lao-kay, about 150 km. southeast of Mengtze. Within China it ranges from western Yunnan through southern Kweichow, to Kwangsi and Kwangtung. Of the two species *H. tibeticum* is restricted to southeastern Tibet, about N. Lat. 29°, while *H. biaristatum* ranges from northeastern Burma to Kwangtung and extends south into Tonkin; it does not seem to occur north of N. Lat. 25°.

The two species now known of the new genus were originally both referred to the genus *Styrax* to which the flowers bear a great resemblance, but the fruit is entirely different. In *Styrax* the fruit is indehiscent or irregularly dehiscent and contains only one or two rather large subglobose or ellipsoid seeds, while the fruit of *Huodendron* resembles strongly that of some Saxifragaceae-Hydrangeae, as *Deutzia* and *Hydrangea*, in shape and size and dehiscence of the capsule and in the numerous scobiform seeds; also the divided style recalls Saxifragaceae, and in some species of *Deutzia* the flattened filaments are elongated beyond the anther or are dentate at the apex. The petals and stamens fall off separately after anthesis, though in bud they are cohering at the very base; in Styracaceae free stamens and petals are very rare. Any doubt, however, one might have in regard to the affinity of *Huodendron*, is convincingly set at rest by the nodal structure of the stem, which shows the unilacunar nodes characteristic of all Ebenales, while the Rosales have trilacunar or quinquelacunar nodes, as pointed out by Dr. I. W. Bailey to whom I am indebted for the examination of the stem.

As type of the genus I have selected *Huodendron tibeticum*, because this species represents the distinctive characters from *Styrax* and other allied genera in a more pronounced degree, particularly by the deeply divided style and by the absence of stellate or fascicled pubescence and also in the distinctly corymbose inflorescence.

For the loan of additional specimens supplementing the material in the herbarium of the Arnold Arboretum (A. A.), I am indebted to Dr. E. D. Merrill of the New York Botanical Garden (N. Y.), Dr. H. L. Mason of the University of California (U. Calif.) and to Sir William Wright Smith of the Royal Botanic Garden of Edinburgh (Edinb.).

I take pleasure in associating with this new genus the name of Dr. H. H. Hu, director of the Fan Memorial Institute of Peiping, one of the foremost and active Chinese botanists, who has contributed and is still contributing extensively to our knowledge of the flora of China.

***Huodendron tibeticum* (Anthony), comb. nov.**

Styrax tibeticus Anthony in Not. Bot. Gard. Edinb. 15: 245 (1927).

Arbor vel frutex 6–25 m. altus, ramis gracilibus teretibus vel apicem versus leviter complanatis glabris; folia alterna, sed interdum apicem ramulorum versus subopposita, decidua, papyracea, elliptico-ovata vel oblongo-ovata vel ovato-lanceolata, 6–11.5 cm. longa et 2.5–4 cm. lata, longe acuminata apice mucronulata, basi late cuneata, integra, nervis utrinsecus 5–9 utrinque leviter elevatis, costa apicem versus supra leviter

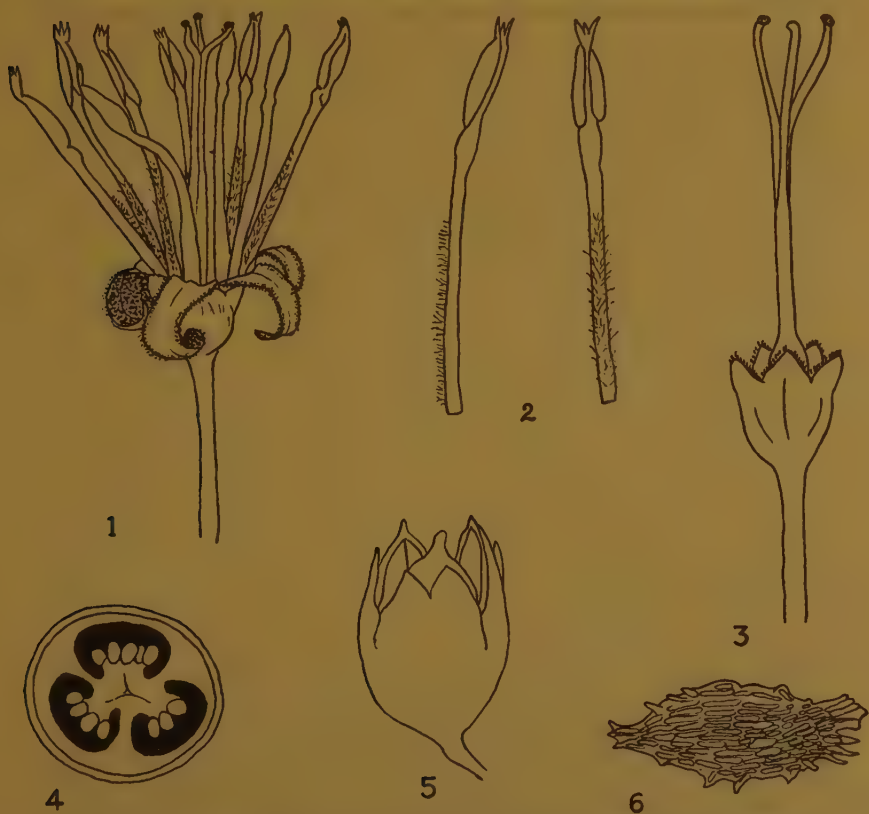


FIGURE 1. HUODENDRON TIBETICUM (Anth.) Rehd. 1. Flower. $\times 7$.—2. Stamens. $\times 8$.—3. Flower with petals and stamens removed. $\times 8$.—4. Cross-section of ovary. $\times 20$.—5. Capsule. $\times 10$.—6. Seed. $\times 35$.

elevata basin versus plana, subtus manifeste elevata; petioli glabri, 5–10 mm. longi, supra leviter canaliculati. Inflorescentia glabra, corymboso-paniculata, terminalis 5–7 cm., lata, laterales cum pedunculo 1.5–3 cm. longo 4–8 cm. longa et 2.5–5 cm. lata; pedicelli graciles, 3–5 mm. longi, ut ramuli glanduloso-verruculosi; calycis tubus cupuliformis, glanduloso-verruculosus, 1 mm. longus, dentibus triangulari-ovatis dimidium tubum

subaequantibus ciliolatis; petala valvata, lineari-oblonga, 6–7 mm. longa et 1–1.5 mm., lata, obtusiuscula, extus tomentosula, intus fere glabra, sub anthesi revoluta; stamina petiolis subaequalonga, filamentis 4–5 mm. longis intus triente inferiore excepto villosis extus glabris, antherae 1.25–1.5 mm. longae, glabrae, apice tridentato circiter 1 mm. longo, dente medio lateralibus plerumque brevior, styli in triente inferiore vel ad medium connati, graciles, glabri; discus glaber. Capsula pedicello plus minusve recurvo suffulta, ovoidea, 3 mm. longa, fusco-brunnea, subinfera; semina brunnea, circiter 1 mm., longa.

SOUTHEASTERN TIBET. T s a r o n g : Salween and Kiu-chiang divide, northwest of Si-chi-to, Lat. $28^{\circ} 35' N.$, Long. $98^{\circ} 30' E.$, alt. 10–11000 ft., *G. Forrest*, no. 21648, June 1922, “shrubby, 20–30 ft., flowers fragrant, white, in open thickets by streams” (holotype in herb. Edinb.); same locality, *G. Forrest*, no. 22882, Oct. 1922 (paratype in herb. Edinb.); Salween and Irrawaddi divide, near banks of Salween at Champutong, forests, alt. 7000 ft., *J. F. Rock*, no. 22020, May–July 1932, tree 70–80 ft. tall, flowers white (A. A., N. Y., U. Calif.); mountains west of Champutong, forests of upper Salween River, alt. 9000 ft., *J. F. Rock*, no. 22474, Oct. 1932 (A. A., N. Y., U. Calif.).

This species has a very restricted distribution and is apparently confined to the mountains of extreme southeastern Tibet between the headwaters of the Irrawaddi and Salween Rivers. In some of its characters, particularly by the deeply divided style and by the absence of stellate or fascicled pubescence is it farther removed from other styraceous genera than the more widely distributed *H. biaristatum*. The fruiting branch of this species has some resemblance to certain species of *Deutzia*.

Huodendron biaristatum (W. W. Sm.), comb. nov.

Styrax biaristatus W. W. Smith in Not. Bot. Gard. Edinb. 12: 233 (1920).—C. E. C. Fischer in Kew Bull. Misc. Inform. 1933: 365.

Frutex vel arbor 6–12 m. altus, ramis gracilibus hornotinis initio tomentosulis demum glabrescentibus, vetustioribus flavido-cinereis vel fusco-cinereis cortice demum rimoso vel fibroso vestitis. Folia alterna, papyracea, oblonga vel elliptico-oblonga vel obovato-oblonga, 8–17 cm. longa et 2.5–6 cm. lata, acuminata, basi cuneata, margine minute et remote denticulate vel integra, supra luteo-viridia, opaca, costa fasciculato-pilosula excepta glabra, subtus vix pallidiora, axillis saepe barbulatis exceptis glabra, costa supra leviter impressa subtus elevata, nervis utrinsecus 5–9 arcuatis margine anastomosantibus supra vix infra manifeste elevatis, venulis subtus elevatis; petioli 6–15 mm. longi, supra tantum vel undique fasciculato-pilosi. Inflorescentiae terminales et axillares, paniculatae, multiflorae, 3–10 cm. longae, ebracteolatae, cinereo-

tomentellae; pedicelli 2–5 mm. longi; calyx cupuliformis, tomentellus, tubo 1–1.5 mm. longus, dentibus late triangularibus acutiusculis tubo brevioribus; petala imbricata, anguste oblonga, 6–9 mm. longa et 2–2.5 mm. lata, utrinque tomentella; stamina petalis subaequilonga, filamentis compressis utrinque dense pilosulis circiter 3 mm. longis, antheris glabris 2 mm. longis connectivo dorso puberulo in appendicem tridentatum vel rarius bidentatum elongata dentibus lanceolatis acutis medio plerumque minore; stylus staminibus paullo longior, crassus dense pilosulus, apice 3-lobata; ovarium semisuperum. Capsula ovoidea, resupinata, 4–5 mm. longa, cinereo-tomentella, in triente superiore sepalis persistentibus cincta; semina 1–1.25 mm. longa, flavo-fusca.

CHINA. Y u n n a n : in thickets in ravines on the western flank of the Shweli-Salween divide, Lat. $25^{\circ} 40' N.$, alt. 9000 ft., *G. Forrest*, no. 18020, May 1919, "shrub 20–30 ft., flowers fragrant, creamy-yellow" (syntype in herb. Edinb.); side valleys of the Shweli-Salween divide, Lat. $25^{\circ} N.$, alt. 8000 ft., *G. Forrest*, no. 17894, June 1919, "shrub 10–20 ft., flowers immature" (Edinb., A. A.); N'Maikha-Salween divide, at Ho-tou, in thickets and open forests, Lat. $25^{\circ} 55' N.$, alt. 7–8000 ft., *G. Forrest*, no. 18400, Aug. 1919, "shrub 12–18 ft., in fruit" (syntype in herb. Edinb.); same locality, *G. Forrest*, no. 18833, Nov. 1919 (syntype in herb. Edinb.); Mengtze, S. E. mountain forests, 6000 ft., *A. Henry*, no. 10764 "tree 15 ft." (syntype in herb. Edinb., A. A., N. Y.); Mengtze, *A. Henry*, no. 13662A, "shrub 10 ft." (syntype in herb. Edinb.; A. A., N. Y.); south of Red River, *A. Henry*, no. 13662, "tree 40 ft." (syntype in herb. Edinb.; A. A.); Shweli-Salween divide, Lat. $25^{\circ} 10' N.$, Long. $98^{\circ} 50' E.$, alt. 9000 ft., in open thickets and forests, *G. Forrest*, no. 26108, Dec. 1924, "tree 30–40 ft." (Edinb., N. Y.); without precise locality, *G. Forrest*, no. 26108, 1924–25 (Edinb., N. Y.). K w e i c h o u : Waichai, Tuh-shan, near border of Kwangsi, alt. 330 m., in densely shaded ravine, *Y. Tsiang*, no. 6686, Aug. 25, 1930, "tree 6 m., diam. of trunk 12 cm., bark pale gray" (A. A.). K w a n g s i : Chin-fong, Lin-yuin-hsien, valley forest, alt. 1300 m., *Steward & Cheo*, no. 336, May 6, 1933, "tree 7 m., flowers white, fragrant" (A. A., N. Y.); Ta-tse-shan, Yung-hsien, forest, alt. 540 m., *Steward & Cheo*, no. 843, Aug. 21, 1933, "tree 9 m., fruit gray" (A. A., N. Y.).

BURMA: Myitkyina Distr., Htangan, 3100 ft., *Sukoe* per *C. E. Parkinson*, no. 9197; Pyet Pass, 7200 ft., *Sukoe* per *C. E. Parkinson*, no. 10115 (ex *C. E. C. Fischer*, l. c.).

TONKIN: route de Lao-kay à Chapa, alt. 1500 m., *A. Petelot*, no. 3803, Aug. 1930 (N. Y.); massif du Fan-tsi-pou, chemin du col de Lo-qui-ho, environs de Chapa, alt. 1400 m., *A. Petelot*, no. 4373, Sept. 1931 (N. Y.).

This species is readily distinguished from *H. tibeticum* by the pubescent inflorescence, the thicker texture of the leaves, the pubescent stout style 3-lobed only at the apex, the shorter filaments pubescent on both sides, the broader narrowly imbricate petals pubescent on both sides and the tomentulose capsules. The fact that the petals in one species of this genus are valvate and in the other imbricate is not unusual in *Styracaceae*, for both kinds of aestivation are found in *Styrax*. The stamens are mostly 3-toothed at the apex, but the middle one is often shorter than the lateral ones; two teeth, as implied by the specific epithet, are only occasionally found.

The leaves of *H. biaristatum* show some variation in dentation, texture, pubescence and in the number of veins. The Forrest specimens have remotely denticulate leaves and are of rather thin texture, the leaves of the Henry specimens are occasionally furnished with minute denticulations reduced to a mucro, but are mostly entire like the other specimens and like those are of thicker chartaceous or subcoriaceous texture. The midrib is usually impressed and puberulous like the petiole, but in Petelot 4373 from Tonkin the midrib is glabrous except slightly puberulous toward the base and slightly elevated and quite glabrous toward the apex, also the lateral veins are slightly elevated and number about 5 pairs, while the leaves of the other specimens have mostly 6 or 9 pairs; by these characters this Petelot specimen approaches the following variety and connects it with the typical form.

***Huodendron biaristatum* var. *parviflorum* (Merrill), comb. nov.**

Styrax parviflora Merrill in Jour. Arnold Arb. 8: 15 (1927).

A typo recedit praecipue ramulis foliis petiolisque glabris foliis magis coriaceis integris nervis utrinsecus 4-6, costa media nervisque supra glabris et elevatis, venulis subtus minus conspicuis.

CHINA. K w a n g t u n g : Lung-t'au Mountain, near Iu, in forest, Canton Christian College, nos. 12070 (holotype in hb. N. Y.; A. A.) and 12349 (paratype in hb. N. Y.; A. A.).

The flowers and fruits of the Kwangtung specimens, as far as can be judged from the rather poor material, are identical with those of typical *H. biaristatum* and the difference in the leaves does not seem sufficient to separate the Kwangtung form as a distinct species, considering the fact that the leaves of *H. biaristatum* show considerable variation and transitions to this variety.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.



PLANTAE SINENSIS

Exsiccatae in the University of California Herbarium and Garden in Berkeley, China

Flora of Szechwan, Tibet

Huodendron tibeticum (Anth.) Rehd.

Shrub 75-80 feet tall; flowers white.

Common in the Himalayas, Tibet, China, India.

Altitude 1000 feet.

Mt. Kanchung, eastern and western slopes, Szechwan and Yunnan.

Joseph H. Rose, No. 1.

May-July 1901.

HUODENDRON TIBETICUM (Anth.) Rehd.



HUODENDRON BIARISTATUM (W. W. Sm.) Rehd.

STUDIES IN THEACEAE, I
EURYA SUBGEN. TERNSTROEMIOPSIS

CLARENCE E. KOBUSKI

With plate 153

DURING the past year the author has been making a survey of the Old World Theaceae, starting with a critical study of the genus *Eurya*.

The genus as a whole has presented some rather difficult problems in specific delimitation and in synonymy which cannot be settled until more ample material or photographs of types deposited in various foreign herbaria can be had.

In Szyszyłowicz's treatment,¹ *Eurya* comprises three sections: *Cleyera* (DC.), *Freziera* (Sw.) and *Proteurya* Szysz. In 1896, Urban² separated *E. sandwicensis* from *Proteurya* and made it the type of the new genus, *Ternstroemiopsis*. The following year Engler³ united *Ternstroemiopsis* with *Eurya* as a new subgenus, elevating, at the same time, the three sections of Szyszyłowicz to subgeneric rank. At present, however, *Eurya* is generally considered as containing but two subgenera, *Proteurya* and *Ternstroemiopsis*, while *Cleyera* and *Freziera* represent distinct genera, the former Asiatic and American, the latter exclusively American.

In this paper, the subgenus *Ternstroemiopsis* is considered. This is distinguished from the subgenus *Proteurya* by the spiral arrangement of its leaves, the thick glandular sepals, fleshy petals and stamens whose anthers are twice as long as the filaments. *Proteurya* is characterized by two-ranked leaves, petals more or less membranous and anthers as long as or shorter than the filaments. Geographically also *Ternstroemiopsis* is distinct being confined solely to the Hawaiian Islands while *Proteurya*, although found in nearly all the Pacific islands and Asia, does not invade the Hawaiian group with a single species.

The institutions from which material for this study was borrowed along with the abbreviations used in this paper, are as follows: herbarium of the Arnold Arboretum of Harvard University (AA), herbarium of Otto Degener (D), Gray Herbarium of Harvard University (Gr), herbarium of the New York Botanical Garden (NY).

¹Szyszyłowicz in Engler & Prantl, Nat. Pflanzenfam. III. 6: 189 (1893).

²Urban in Ber. Deutsch. Bot. Gesell. 14: 49 (1896).

³Engler in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 1: 247 (1897).

KEY TO THE SPECIES AND VARIETIES

- A. Leaves subcordate or truncate at base, obtuse or rounded at apex
 - B. Small trees or erect shrubs1. *E. sandwicensis*
 - BB. Prostrate shrubs1a. *E. sandwicensis* var. *prostrata*
- AA. Leaves cuneate at base, acute at apex
 - C. Leaves 3.5-4.7 cm. long, 1.2-1.7 cm. wide.....2. *E. Degeneri*
 - CC. Leaves either larger or smaller than C
 - D. Leaves 5.3-8.7 cm. long, 2.5-3.5 cm. wide
 - 2a. *E. Degeneri* f. *grandifolia*
 - DD. Leaves 3.0-4.5 cm. long, 0.7-1.2 cm. wide
 - 2b. *E. Degeneri* f. *stenophylla*

1. ***Eurya sandwicensis*** A. Gray, Bot. U. S. Expl. Exped. 1838-1842, 1: 209 (1854). — H. Mann in Proc. Amer. Acad. Arts Sci. 7: 156 (Enum. Hawaiian Pl.) (1867); Mem. Boston Soc. Nat. Hist. 1: 534, 539 (1869). — Hillebrand, Fl. Haw. Isl. 41 (1888). — Drake del Castillo, Ill. Fl. Ins. Maris Pacif. 117 (1890). — Szyszylowicz in Engler & Prantl, Nat. Pflanzenfam. III, 6: 190 (1893). — A. A. Heller in Minn. Bot. Studies, 1: 856 (1897). — Rock, Indig. Trees Haw. Isl. 308 (1913). — Melchior in Engler & Prantl, Nat. Pflanzenfam. Ed. 2, 21: 147 (1925).

Eurya sandwicensis A. Gray var. *sessilifolia* A. A. Heller in Minn. Bot. Studies, 1: 856 (1897), as a synonym.

Ternstroemiopsis sandwicensis Urban in Ber. Deutsch. Bot. Ges. 14: 49 (1896).

Small trees, 5-6 m. in height, occasionally shrubby in higher altitudes, 2-3 m.; branches crowded with leaves, ultimate branchlets strigose; leaves oblong, elliptical or obovate, coriaceous, glabrous, occasionally strigosely hairy on midrib, 4.5-9.0 cm. long, 1.5-3.7 cm. wide, on short petioles 2-3 mm. long, sometimes subsessile, obtuse or rounded at the apex, more or less cordate, occasionally truncate at the base, closely serrulate with inflexed mucronulate teeth, veins and veinlets finely reticulate beneath, reddish brown in color; flowers solitary, occasionally two in axils, nodding, ebracteolate, pedicels approximately 5 mm. long; calyx purplish brown, quite coriaceous, subtended by two small unequal bracts; sepals five, unequal, 3-4 mm. long, persistent, suborbicular, thick in central portion, membranous, lighter in color and slightly glandular on margin, occasional strigose hairs on external surface; corolla pale yellow or cream-color, imbricated; petals five, obovate, 5-6 mm. long, united at base, somewhat fleshy in central portion; stamens in staminate flowers 10-15, slightly adnate to base of corolla, filaments distinct, half as long as the oblong mucronate anthers; staminodia in pistillate flowers, five sometimes six, 2-3 mm. long; pistil having three or occasionally

four styles, sometimes connate nearly to stigma, usually divided; stigmas three (or four); ovary glabrous, 3-celled, axial placentation; fruit a globose berry, 7–10 mm. across, dark blue-black, many-seeded; mature persistent, subcordate calyx-lobes 8 mm. long, 7.5 mm. across at widest portion, lobes at base lighter in color and more membranous.

SPECIMENS EXAMINED:

HAWAIIAN ISLANDS. O a h u : Nuuanu-Pali, *U. Faurie*, no. 284, October 1909 (AA); on mountains behind town of Honolulu, *Wm. Rich*, collected in 1840 (type) (Gr, NY); exact locality lacking, *M. J. Remy*, no. 562, collected 1851–1855 (Gr); data lacking, *M. J. Remy* (NY); exact locality lacking, *H. Mann & W. T. Brigham*, no. 524, collected 1864–1865 (Gr, NY); exact data lacking, *W. Hillebrand* (Gr); precise data lacking, *C. Gaudichaud*, collected probably 1836 (Gr); in rain-forest from Kahana church up ridge to summit of mountain south-east of Kahana Bay, *O. Degener*, no. 8680, July 3, 1932 (AA, D); Waipio, Waiawa Ridge, on Dicranopteris-covered ridge, *O. Degener & Dr. C. L. Shear*, no. 9838, March 5, 1928 (tree 15 ft.; fruit inky blue-black) (AA, D); open forest in Dicranopteris tangle, Manana Gulch ridge, *O. Degener, W. Bush & K. K. Park*, no. 8679, October 2, 1932 (AA, D); on and near the summit of Konahuanui, *A. A. Heller*, no. 2240, May 2, 1895 (NY); lower slopes of Konahuanui, above Manoa, *A. A. Heller*, no. 2311, May 13, 1895 (AA, NY, Gr); ridge west of Kalihi valley, *C. N. Forbes*, no. 1483.O, March 17, 1910 (NY); ridge between Pololo and Waialue iki, *C. N. Forbes*, no. 2408.O, January 30, 1917 (NY); Koolau Mts., Pumaluu, *J. F. Rock*, no. 627, December 3–10, 1908 (Gr); Pumaluu, *J. F. Rock*, no. 843, December 1908 (NY); precise data lacking; *J. F. Rock*, collected 1910 (Gr). K a u a i : Mt. Waialeale, alt. 5200 ft., *J. F. Rock*, no. 8864, October 20, 1911 (Gr, NY); along stream-beds, Kaholuamano, *J. F. Rock*, no. 5499, September 1909 (Gr, NY); Kaholuamano, *J. F. Rock*, collected March 3–10, 1909 (NY); Hanapepe, *U. Faurie*, no. 286, December 1909 (AA). M a u a i : Honakahau Drainage Basin, *C. N. Forbes*, no. 421.M, September 25–October 17, 1917 (NY). H a w a i i : Kilauea, near fern-forest, *O. Degener*, no. 8678, November 10, 1929 (AA, D).

In the whole genus this species is probably the most outstanding. Although confined to the Hawaiian group, it has been found in nearly all the islands from which material has been collected. The flowers and fruit are nearly twice the size of any other species. Along with this size character can be mentioned the distinct reddish reticulate veining of the lower surface of the leaf and the subcordate or truncate base of the leaf.

The collections of Otto Degener made during the last few years on

the various islands of the group had great influence in the decision finally to place the majority of Hawaiian specimens in this species. His specimens were so ample that it was possible to make two and even three sheets of each for the herbarium of the Arnold Arboretum. These sets of material show great gradation in leaf-size — a character which might cause some, especially in this genus, to describe new species.

Faurie's specimen, no. 286, according to the collector, was made at Hanapepe, Oahu. This probably is a mechanical error made in transferring the field notes to the herbarium label. Hanapepe is on the island of Kauai and the collection date of no. 286 agrees with other material collected by Faurie on Kauai.

1a. *Eurya sandwicensis* A. Gray var. **prostrata**, var. nov.

A typo recedit habitu prostrato et foliis remotis.

SPECIMENS EXAMINED:

HAWAIIAN ISLANDS. M o l o k a i : At edge of windswept forested pali, Ohialele Pali, *O. Degener*, no. 8676 (type, AA) May 10, 1928 (more or less trailing along ground with branches sometimes eight feet long; flowers yellow, difficult to distinguish plant from *Vaccinium*) (AA, D); Pelekunu trail, *C. N. Forbes*, no. 249.Mo, July 1912 (NY).

A quotation from a recent letter from Otto Degener, the collector of the cited type throws considerable light on this variety and the species *E. sandwicensis* : — "*Eurya*, as I have found it on Oahu, grows as an erect small tree with very dense foliage. It is rare, and where found, usually grows in openings in the lower forest, covered over with *Gleichenia*. Rainfall would be moderate."

"The Molokai specimen I have found nowhere except in a typical dense extremely rainy rain-forest, and curiously enough, not anywhere in that region but only on the brink of a cliff extending for several miles. In short, it grows on the very "backbone" of Molokai where the rain and fog drive violently over the mountain crest. I collected five months on Molokai and do not remember seeing any *Eurya* except in that one type of locality. The rain-forest reaches up to this cliff and it is among the shrubs and small trees immediately overlooking the cliff that the *Eurya* is to be found. The plant sprawls rather than creeps, producing slender branches of unusual length—possibly 12 feet—with its leaves spaced far apart."

The collector remarked further that at first on seeing sterile plants, he thought this variety to be a low-growing *Vaccinium*. However, later on finding flowering material, he discovered it to be an *Eurya*. He suggested it as a variety or possible new species.

The second cited specimen, Forbes no. 249.Mo, resembles the type

in the remoteness of leaves. However the habit of the plant was not given by the collector, but it appears to be prostrate.

2. *Eurya Degeneri*, spec. nov.; a *E. sandwicensis* A. Gray foliis ellipticis 3.5–4.7 (2.5–6.5) cm. longis, 1.2–1.7 (1.2–2.2) cm. latis, apice acutatis et emarginatis, basi cuneatis recedit.

Branches covered with leaves especially at ends, ultimate branchlets sparsely strigose; leaves elliptic, coriaceous, 3.5–4.7 (2.5–6.5) cm. long, 1.2–1.7 (1.2–2.2) cm. wide, acute at the apex, emarginate, cuneate at the base, closely serrulate with inflexed mucronulate teeth, conspicuously reticulate on under surface, veins and veinlets reddish brown in color, especially near base of leaf where color spreads into the leaf; petiole 3 mm. long; mature flowers unknown, bud resembling *E. sandwicensis* sufficiently in coriaceous character and color of calyx with occasional strigose hairs, character and number of stamens and corolla to show it to be typical of the genus and closely related to *E. sandwicensis*; berry (probably not mature) blue-black, 5 mm. across with the persistent styles separate to near the base, 3-celled, axial placentation, many-seeded.

SPECIMENS EXAMINED:

HAWAIIAN ISLANDS. K a u a i : open forest, Waineke swamp Kokee, *O. Degener*, no. 8675 (type AA) July 1, 1926 (AA, D); high plateau of Waimea, Halemanu to Kaholuamano, *J. August Kusche*, nos. 28, 139, 140, collected in 1919 (AA); Kilauea, *U. Faurie*, no. 285, January 1910 (AA); west side Waimea Drainage Basin, Kanaikinaua, *C. N. Forbes*, no. 1016.K, July 3–August 18 (1917) (AA, NY).

This species is very closely allied to *E. sandwicensis*. The leaf characters are most distinctive between the two species. *Eurya Degeneri* has elliptical leaves, cuneate at the base, acute and emarginate at the apex. On the other hand, *Eurya sandwicensis* has leaves which are oblong or elliptic, subcordate or truncate at base and rounded or obtuse at the apex. *Eurya Degeneri* and its varieties are confined to the island of Kauai, while *Eurya sandwicensis* is found on nearly all the islands including Kauai.

Otherwise these two species belonging to this distinctive section of the genus are very similar. This is especially true in flower and fruit characters. Although the mature flowers and fruit were not available in *E. Degeneri*, the material such as it is shows conclusively that there is a great resemblance.

It is a pleasure to dedicate this species to Otto Degener of Hawaii, whose recent collections from the islands are extremely fine and whose material of *Eurya* aided tremendously in clearing up this section.

2a. **Eurya Degeneri** Kobuski forma **grandifolia** (Wawra), comb. nov.

Eurya sandwicensis A. Gray β var. Hillebrand, Fl. Hawaiian Isl. 41 (1888). — Drake del Castillo, Ill. Fl. Ins. Maris Pacif. 117 (1890).

Eurya sandwicensis A. Gray var. *grandifolia* Wawra in Flora, 56: 168 (1873). — J. F. Rock, Indig. Trees Haw. Isl. 308 (1913).

A typo recedit foliis amplioribus, 5.3–8.7 cm. longis, 2.5–3.5 cm. latis.

SPECIMEN EXAMINED:

HAWAIIAN ISLANDS: K a u a i : Wainiha, *U. Faurie*, no. 298, January 1910 (AA).

This large-leaved form has seemed rather evasive to most collectors. Hillebrand, Del Castillo, Wawra and Rock have made reference to it in literature. The first three in their treatments were working with a single specimen, that of Wawra collected at Kealia on the island of Kauai. Incidentally we have only the single specimen collected by Faurie (no. 298) collected at Wainiha. The Faurie specimen was collected on the north coast of Kauai while Wawra made his collection on the west coast.

Rock, although having collected considerably on the islands, never encountered this large-leaved form. However, he collected the narrow-leaved form cited next.

These two forms like the species have distinctly cuneate leaf-bases and acute apices. Their variation from the species lies chiefly in the leaf size. Again, like the species, they are found only on the island of Kauai.

2b. **Eurya Degeneri** Kobuski forma **stenophylla**, forma nov.

A typo recedit foliis minoribus angustioribusque, 3.0–4.5 cm. longis, 0.7–1.2 cm. latis.

SPECIMEN EXAMINED:

HAWAIIAN ISLANDS. K a u a i : precise locality and date of collection lacking, *J. F. Rock*, no. 17274 (type) (AA).

Unfortunately, the Rock specimen cited above is sterile and was placed in this genus under *E. sandwicensis* with some hesitation by an earlier student. At first, I was quite dismayed because I felt that it belonged to a species other than *E. sandwicensis*, but because of the lack of flowers or fruit I hesitated to describe it as new. It was not until more material came to my attention that its true affinity with *E. Degeneri* was discovered.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.



PLANTS OF HAWAII
Eurya degeneri Kobuski

Eurya degeneri Kobuski
C. L. Robinson
Hawaii, 1913

Collected by "Vire" DEGENER.
Hawaii plants described in "Plants Near Nat. Park" and in new illustrated
"Flora Supplement" for "The Botanist" Honolulu, N. H.

EURYA DEGENERI Kobuski

TWO NEW SPECIES OF CRATAEGUS FROM MISSOURI

ERNEST J. PALMER

With two text figures

Crataegus hannibalensis, sp. nov. Arbor 6–8 m. alta vel frutex arborescens 4–6 m. altus, ramulis annotinis gracilibus vel paulo validis glabris fusco-viridibus, spinis numerosis. Folia ovata vel obovata vel oblongo-ovata, serrata, apice acuta, basi cuneata in petiolum 8–12 mm. longum attenuata, 2.5–4 cm. longa, 2–3 cm. lata, surculorum validorum ad 5–6 cm. longa, 4–5 cm. lata, matura firma, crassa, glabra, dentata, nervis superne manifeste impressis. Inflorescentiae glabrae, laxae, plerumque 5–16-florae; flores 14–16 mm. lati, staminibus circiter 10, stylis 1–3 plerumque 2; sepalis lanceolatis integris vel sparse dentatis. Fructus ovoideus, obovoidea-oblongus vel rare subglobosus, 8–10 mm. longus, 7–8 mm. latus, firmus, viridis denique rubro-luteus raro pruinosis, seminibus 2–3 plerumque 2 ovalibus dorso sulcatis.

A tree 6–8 m. tall, or sometimes an arborescent shrub 4–6 m. tall, with intricate ascending or horizontal branches and slender to stoutish flexuous branchlets, glabrous and olive-green or olive-brown at the end of the first season, usually armed with numerous stout, straight or curved purplish thorns 3–6 cm. long. Bark gray or pale brown, slightly scaly. Leaves obovate, oblong-obovate or oval, acutely pointed, short-acuminate or rarely rounded at apex, cuneate at the base and attenuate into the short 8–12 mm. long petioles, sharply serrate usually nearly to the base, glabrous, firm to subcoriaceous at maturity, yellowish-green above and slightly paler beneath, with slender but prominent mid-rib and 5–7 pairs of parallel veins elevated on the under surface and conspicuously impressed above, those of the fruiting branches mostly 2.5–4 cm. long and 2–3 cm. broad, on vigorous sterile shoots often 5–6 cm. long and 4–5 cm. broad, and with margins coarsely serrate or dentate. Flowers in loose glabrous compound 5–16-flowered corymbs, 14–16 mm. in diameter; pedicels slender, often glandular, 1–2 cm. long; stamens about 10; anthers in specimens examined pale yellow; styles 1–3, usually 2; calyx-lobes lanceolate, entire or slightly serrate towards the base, glabrous without and glabrous or slightly villous within. Fruit oval, oblong-obovoid or rarely nearly globose, 8–10 mm. long, 7–8 mm. thick, hard and green until late in the season, turning dull red or orange-red and becoming mellow when fully ripe late in September, rarely with a

slight pruinose bloom. Fruiting calyx sessile or slightly elevated, with a broad shallow cavity; calyx-lobes often persistent and appressed, flesh thin; nutlets 1-3 but usually 2, relatively large, oval or elliptic in outline, blunt or rounded at the ends, and with broad shallow ridges and grooves on the dorsal surface.



FIGURE 1. *CRATAEGUS HANNIBALENSIS* E. J. Palmer. $\times 2/3$

Thickets and borders of woods, in fertile soil, on limestone hills or often along bluffs and banks of streams. *Crataegus hannibalensis* is rather abundant in northern Missouri and southeastern Iowa, and it is probably more widely distributed. A specimen collected in western Ohio seems to belong here.

This species is conspicuous and easily distinguishable on account of its rather large (for the group) yellowish-green leaves with deeply impressed veins, the pale olive branchlets and comparatively small oval or oblong fruit. In their deeply impressed veins the leaves resemble somewhat certain species of the *Punctatae* group, but the characters of the fruit and flowers and the entire absence of pubescence seem to place it

clearly in the *Crus-galli* group. The type specimen is in the herbarium of the Arnold Arboretum.

Missouri: Hannibal (Marion Co.), *John Davis*, no. 177, Oct. 6, 1911, May 14, Oct. 10, 1912, Oct. 13, 1913; *E. J. Palmer*, no. 20381, Sept. 7, 1921; no. 20382 (type), Sept. 7, 1921; no. 20405, Sept. 8, 1921; no. 22337, Oct. 24, 1922; south of Hannibal (Ralls Co.), *John Davis*, no. 1645, Oct. 4, 1916; Eolia Pike Co., *John Davis*, no. 25, Sept. 30, 1912; no. 2147, Sept. 20, 1913; no. 2149, Sept. 22, 1913; no. 2153, Sept. 21, 1913; Dumas, Clark Co., *B. F. Bush*, no. 10139, July 28, 1923; between Renick and Clark, Macon Co., *E. J. Palmer*, no. 35943, May 21, 1929; between Lancaster and Downing, Schuyler Co., *Palmer & Steyermark*, no. 40970, June 30, 1933; Mill Grove, Mercer Co., no. 41270, July 4, 1933; Shelbina, Shelby Co., no. 40865, June 28, 1933; Eagleville, Harrison Co., no. 41340, July 6, 1933; St. Francois Co., *C. S. Sargent*, Oct. 5, 1899. **Ohio:** Springfield, *R. E. Horsey*, no. 338, May 17, Oct. 25, 1915. **Iowa:** Keokuk, Lee Co., *E. J. Palmer*, no. 21829, Sept. 6, 1922; no. 21831, Sept. 6, 1922; no. 40595, June 25, 1933; Burlington, Des Moines Co., *E. J. Palmer*, no. 21800, Sept. 6, 1922.

***Crataegus Danielsii*, sp. nov.** Arbor 6–7 m. alta vel frutex arborescens 4–6 m. altus. Folia oblongo-ovata, elliptica vel rhombica, grosse serrata, saepe supra medium obscure inaequaliter incisa, apice acuta vel acuminata, basi cuneata in petiolum gracillimum 8–15 mm. longum attenuata, matura papyracea sed firma, superne glabra, infra paulo villosa, 2.5–4 cm. longa, 1–2.5 cm. lata, ramulorum sterilius ad 5–6 cm. longa 3–5 cm. lata. Inflorescentiae laxae, ramosae, paulo villosae, 6–15-florae, bracteis linearibus glanduloso-serratis. Flores 14–16 mm. lati, staminibus circa 12–15, antheris rubicundis, stylis 2–4, plerumque 3, sepalis lineari-lanceolatis integris vel paulo glanduloso-serratis. Fructus subglobosus, 8–12 mm. latus, maturus rubicundus; seminibus 2–3 dorso sulcatis.

A tree 6–7 m. tall, or sometimes an arborescent shrub 4–6 m. tall, with erect or ascending intricate branches and slender branchlets, more or less villous when young in the typical form, and armed with slender thorns 2–3 cm. long. Leaves oblong-elliptic, oblong-obovate or narrowly rhombic in outline, sharply and irregularly serrate, often obscurely incised above the middle with one or more pairs of shallow lobes or unsymmetrical with one or more odd lobes, pointed or acuminate at the apex, attenuate at the base into the slender 1–1.5 cm. long petioles, usually red as they unfold, and then villous on both surfaces, thin but firm at maturity, glabrous above and more or less villous along the veins beneath, those of the fruiting branches mostly 2.5–4 cm. long and 1–2.5

cm. broad, and up to 5-6 cm. long and 3-5 cm. wide on vigorous sterile shoots; petioles usually sparsely villous, sometimes with a few scattered glands. Flowers 14-16 mm. in diameter, in loose slightly villous compound corymbs; pedicels slender, 8-15 mm. long, glabrous or sparsely villous; bracts numerous and conspicuous, narrowly linear, finely glandular-serrate on the margins; stamens usually 12-15; anthers pink or rose-color in specimens examined; styles 3-4, usually 3; calyxlobes linear-lanceolate, entire or somewhat glandular-serrate towards



H. B. Root.

FIGURE 2. *CRATAEGUS DANIELSII* E. J. Palmer. $\times 2/3$

the base. Fruit subglobose, 8-12 mm. in diameter, pruinose, becoming dull crimson when ripe in late September or October, flesh thin and hard; nutlets 2-3, usually 3, oblong, rounded at the ends and with broad shallow grooves and ridges on the dorsal surface.

Limestone glades and hillsides in the vicinity of Columbia, Missouri.

Several trees referable to this species have been found, all so far as known within a few miles of the type locality. The extremely local distribution, the variable and often asymmetrical outline of the leaves and the sparse and variable pubescence, nearly or quite absent in some specimens, all suggest the possibility of a hybrid origin, and it may have

originated as a cross between *Crataegus crus-galli* and *C. verruculosa*, both of which are growing in the immediate vicinity. The specific name is for Dr. Francis Daniels, author of a Flora of Columbia, Missouri, and vicinity, who first collected it there.

M i s s o u r i : near Columbia, Boone Co., Hawthorn glades, north of Columbia, *Francis Daniels*, Sept. 26, 1902; May 3, 1903; *W. H. Rickett*, no. 8 (Crat. #8), 50 yds. west of Balanced Rock, May 3, 1931; no. 36 (Crat. #35), north side of Walnut St., west of highway 63, May 6, 1931; *Francis Drouet* (Crat. #8, W. H. R. #107), 50 yds. west of Balanced Rock, Oct. 4, 1931; (Crat. #8, W. H. R. #69), west of Balanced Rock, Sept. 15, 1931; (Crat. #35, W. H. R. #71), north side of Walnut St., west of highway 63, Sept. 22, 1931; *E. J. Palmer*, no. 39265 (type), May 4, 1931; near Hinton, Boone Co., *W. H. Rickett*, no. 40 (Crat. #39), 4.4 miles north of Hinton, May 17, 1931; no. 43 (Crat. #42), 1.3 miles south of Hinton, May 17, 1931; 84 (Crat. #54), 3.6 miles north of Hinton, Sept. 31, 1931; no. 86 (Crat. #56), north of Hinton, Sept. 30, 1931; no. 88 (Crat. 42), 1.3 miles south of Hinton, Sept. 30, 1931; no. 91 (Crat. #43), 2.3 miles south of Hinton, Sept. 30, 1931. Type in the herbarium of the Arnold Arboretum. All other specimens examined are in the herbarium of the University of Missouri.

In a few specimens examined the young foliage, branches, and inflorescence are quite glabrous and in others there is only the slightest trace of pubescence in the form of a few scattered hairs on either the pedicels, petioles or veins of the leaves. This may be distinguished as *Crataegus Danielsii* f. **glabra**, f. nov.¹

Thickets, limestone hills and glades, Boone County, Mo. With the type.

W. H. Rickett, no. 39 (Crat. #38), 4.4 miles north of Hinton, Mo., May 17, 1931, in the herbarium of the University of Missouri, may be taken as the type of this form.

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¹A typo differt ramulis foliis inflorescentiis glabris vel raro leviter pilosis.

NEW HYBRIDS FROM THE ARNOLD ARBORETUM

EDGAR ANDERSON AND ALFRED REHDER

× *Akebia pentaphylla* (Mak.) Makino in Tokyo Bot. Mag. 16: 30 (1902) = *A. quinata* Dcne. × *trifoliata* (Thbg.) Koidz.

Akebia trifoliata var. *pentaphylla* Makino in Tokyo Bot. Mag. 5: 329 (1891).

Artificial hybrids between *Akebia trifoliata* Koidz. and *A. quinata* Dcne. were produced at the Arnold Arboretum in 1932 by Dr. Karl Sax.¹

Though they have not yet flowered the hybrid seedlings have now reached a stage where their intermediate character is clearly evident and is in close agreement with Makino's description (l. c.) of × *A. pentaphylla*, a putative hybrid widely distributed in Japan. The hybrids, on the whole, resemble *A. trifoliata* somewhat more closely than they do *A. quinata*. As yet many of the leaves are three-foliolate, although leaves with four and five leaflets have been produced. It is of interest that Makino originally considered × *A. pentaphylla* as a variety of *A. trifoliata* (l. c.). In this connection one might speculate as to the origin of *A. trifoliata* Koidz. var. *australis* (Diels) Rehd. Diels² in describing the variety commented on its extreme variability, and it occurs in a region where both *A. trifoliata* and *A. quinata* are native. Furthermore, it is intermediate between the two species in both leaf and flower, though resembling *A. trifoliata* more closely. It seems not impossible that it has resulted through extensive hybridization between *A. trifoliata* and *A. quinata* in a region where the former is relatively more abundant.

It should be remembered that the consequences of hybridization between two species may be quite different in different parts of their ranges, depending upon the relative frequency of the two species, the presence of polyploid races within either parent, the adaptability of the hybrid to local conditions, etc. Such matters are usually highly speculative. The production of an artificial hybrid will make it possible, ultimately, to study such questions experimentally in the genus *Akebia*.

E. A.

Prunus Juddii E. Anderson, hybr. nov. = *P. Sargentii* Rehd. ♀ × *yedoensis* Mats. ♂.

¹Arnold Arb. Bull. ser. iv. 2: 17-20 (1934). — They are growing in the Arboretum under no. 624-32 and specimens collected June 3, 1935 are preserved in the herbarium.

²Bot. Jahrb. 29: 344 (1900).

Intermedia inter parentes, et ab utroque differt praecipue inflorescentiis 2-6-floris breviter racemosis et breviter pedunculatis, calycis lobis sparse et leviter glanduloso-serratis, stylo basi sparse piloso.

Growing in the Arnold Arboretum under no. 22489 and type specimens collected May 5 and 10 and June 3, 1935, are preserved in the herbarium.

An upright tree with spreading branches. Branchlets glabrous. Leaves ovate, acuminate, doubly serrate, dull brownish green when unfolding, glabrous throughout. Flowers before the leaves in very short-peduncled racemes of two to six, subtended by greenish bracts. Pedicels with weak scattered hairs at the base. Petals oblong, white or whitish, flushed with deep rose pink (Ridgway). Calyx-tube cylindric to sub-urceolate, glabrous. Calyx-lobes weakly and irregularly glandular-serrate. Style with scattered hairs at the base. Fruit black.

Among the seedlings of *Prunus Sargentii* Rehd. (*Prunus serrulata* Lindl. var. *sachalinensis* [F. Schmidt] Mak.) which have been raised from the original trees at the Arnold Arboretum were certain plants which are evidently hybrids between that species and other cherries which were flowering at about the same time. In the case of one of these specimens the evidence for its exact parentage is so clear and the hybrid tree promises to be of such horticultural importance for New England that it seemed desirable to provide the hybrid with a scientific name.

I take pleasure in naming the hybrid after the propagator for the Arnold Arboretum, Mr. W. H. Judd, whose precise record of the material which has passed through his department is of great scientific importance.

The hybrid originated in 1914 at the Arnold Arboretum as a seedling of one of the original trees of *Prunus Sargentii* raised from seed sent from Japan by Dr. W. S. Bigelow in 1890. *Prunus yedoensis* was acquired in 1902 and for many years a large specimen stood adjacent to *Prunus Sargentii*, no. 5777. Since their flowering dates usually overlapped it is not at all surprising that cross-fertilization should have taken place. Mr. Edwin L. Hillier of the West Hill Nurseries, Winchester, England, writes me that he has obtained similar hybrids from seed sent him from the Arnold Arboretum. Since seed of both *Prunus yedoensis* and *P. Sargentii* have been distributed very widely for a number of years by the Arnold Arboretum, it is quite possible that the hybrid may have turned up in a number of nurseries and gardens.

× *Prunus Juddii* has proved hardy during the last two phenomenally cold winters though it is planted at the edge of one of the coldest spots in the Arnold Arboretum. It furthermore holds its flowers longer than does *P. Sargentii* and is a thrifty quick-growing tree. From *P. Sargentii*

it can most easily be distinguished by the greener young leaves, by the scattered hairs at the bases of the style and the pedicel, and by the glandular serrations of the calyx. From *P. yedoensis* it can be distinguished by its brighter flowers and by its glabrous calyces and leaves. A more complete comparison of the hybrid and the parental species is given in Table I.

TABLE I. COMPARISON OF \times *PRUNUS JUDDII* WITH ITS PARENTS

<i>P. yedoensis</i>	\times <i>P. Juddii</i>	<i>P. Sargentii</i>
branches spreading to horizontal	branches spreading	branches upright
leaves greenish when unfolding	leaves dull brownish green when unfolding	leaves bright bronze green when unfolding
flowers in 2-6-flowered short-peduncled racemes	flowers in 2-4-flowered very short peduncled racemes	flowers in sessile or sub-sessile clusters
pedicels finely pubescent	pedicels with weak scattered hairs at the base	pedicels glabrous
petals broadly oblong, nearly white	petals oblong, flushed with rose pink	petals narrowly oblong, typically bright rose pink
calyx tube urceolate-cylindric, finely pubescent	calyx tube sub-urceolate, glabrous	calyx tube cylindric-campanulate, glabrous
calyx-lobes strongly glandular-serrate	calyx-lobes weakly and irregularly glandular serrate	calyx-lobes entire
style pubescent	style with scattered hairs at the base	style glabrous

Since it has not been found wild, *Prunus yedoensis* has itself been thought to be a hybrid between *Prunus Lannesiana* and *Prunus subhirtella*.¹ The fact that it comes true from seed² makes this hypothesis less likely, though such true-breeding hybrids are not unknown in the genus *Prunus*.³

E. A.

\times *Viburnum Juddii* Rehder, hybr. nov. = *V. Carlesii* Hemsl. ♀ \times *bitchiense* Mak. ♂.

A *Viburno Carlesii* praecipue differt foliis supra minus dense pilosis, petiolis paullo brevioribus, corymbo laxiore magis multifloro, corolla extus magis roseo suffusa graciliore, limbo paullo minore, lobis angustioribus filamentis quam antherae longioribus; A *V. bitchiense* differt praecipue foliis supra magis pilosis, petiolis paullo longioribus, 5-7 mm. longis, corymbo 6-7 cm. diam. magis florifero, corollis majoribus tubo

¹Wilson, E. H. The Cherries of Japan, p. 19. Cambridge (1916).

²Russell, Paul. The Oriental Flowering Cherries, p. 19. Washington (1934).

³C. D. Darlington in Jour. Genet. 19: 213-256 (1928).

9-10 mm. longo, limbo 14-15 mm. diam., lobis paullo latoribus circiter 5 mm. latis, staminibus medio tubo affixis antheris faucem attingentibus.

Growing in the Arnold Arboretum under no. 447-20; type specimens collected May 14, 1929, May 9, 1930, May 14, 1931 and May 14, 1935.

This hybrid is in almost all characters intermediate between the parent species which are closely related and very similar, the chief difference being in the stamens which in *V. bitchiuense* are inserted in the lower fourth or third of the corolla-tube with the filaments about twice as long as the anthers and the tips of the latter 1.5-2 mm. below the mouth of the corolla-tube, while in *V. Carlesii* the stamens are inserted above the middle with the filaments as long or shorter than the anthers which reach the mouth of the corolla-tube. Table II shows the chief characters by which the hybrid may be distinguished from the parent.

TABLE II. COMPARISON OF *VIBURNUM JUDDII* WITH ITS PARENTS

	<i>V. bitchiuense</i>	× <i>V. Juddii</i>	<i>V. Carlesii</i>
Leaf	broad ovate to ovate or elliptic, sparingly furcate-pilose above, slightly lustrous above and usually rugose	ovate to ovate-oblong or elliptic, furcate-pilose above, bright green, not rugose	ovate to oblong-ovate, rather densely furcate-pilose and grayish green when young, not rugose
Petiole	2-7 mm. long	4-9 mm. long	5-12 mm. long
Inflor-escence	4-5 cm. across, rather loose, rays 7-12 mm. long, slender	6-8 cm. across, rather loose, rays about 1.5 cm. long, slender	4.5-6 cm. across, compact, rays 5-8 mm. long, stout
Corolla	pink outside, tube 7-8 mm. long, limb 12-14 mm. across, lobes 4-5 mm. broad	pink outside, tube 9-10 mm. long, limb 15-16 mm. across, lobes about 5 mm. broad	corolla faintly flushed pink outside, tube 7-8 mm. long, limb 15-16 mm. across, lobes 5-6 mm. broad
Filaments	inserted in the lower third of the corolla tube, about twice as long as anthers	inserted about or slightly below the middle, about 1-½ as long as anthers	inserted above to near the middle as long or slightly longer than anthers
Anthers	tips 1.5-2 mm. below the mouth	tips reaching the mouth	tips reaching the mouth

As shown by the table above, the hybrid holds the middle between the two parent species except in the size of the inflorescence and the length of the corolla-tube, in which it exceeds both parents. In its general appearance it resembles more *V. bitchiuense* on account of its looser habit and the looser inflorescence and more brightly pink flowers. As an ornamental plant it is superior to either parent.

Viburnum Juddii was raised in 1920 by Mr. William H. Judd of the Arnold Arboretum staff from seed of *V. Carlesii*. The largest plant of the hybrid is now 2 m. tall and flowered for the first time in 1929. Like the parent species it has stood the severe cold of the last two winters without injury to its flower-buds.

A. R.

× *Syringa diversifolia* Rehder, hybr. nov. = *Syringa pinnatifolia* Hemsl. ♀ × *oblata* Lindl. var. *Giraldii* (Lemoine) Rehd. ♂.

A *Syringa pinnatifolia* differt praecipue foliis partim integris, partim basi pinnatifidis pinnis 1-4 ovato-oblongis vel anguste ovatis 2-3 cm. longis acuminatis basi anguste decurrentibus leviter ciliolatis ceterum glabris, foliolo terminali ovato-oblongo sensim acuminato 3.5-5 cm. longo, foliis integris ovato-oblongis, 3.5-5 cm. longis, 1.4-2.2 cm. latis, basi rotundatis, inferioribus interdum fere ovatis, inflorescentia ad 12 cm. longa et laxiore, corolla coeruleo-lilacina, tubo circiter 8 mm. longo, limbo circ. 1 cm. diam., lobis apice leviter cucullatis, antheris faucem paene attingentibus; a *S. oblata* var. *Giraldii* recedit praecipue foliis partim pinnatifidis minoribus et angustioribus, gemma terminali ramorum evoluta et ramum foliiferum emittente, inflorescentia minore, corollae tubo brevior et limbo angustior, antheris faucem attingentibus.

Growing in the Arnold Arboretum under no. 148-30; type specimens collected May 17 and 21, 1935, preserved in the herbarium.

A comparison of the chief characters by which the hybrid differs from its parents are given in Table III.

TABLE III. COMPARISON OF SYRINGA DIVERSIFOLIA
WITH ITS PARENTS

	<i>S. pinnatifolia</i>	<i>S. diversifolia</i>	<i>S. oblata</i> var. <i>Giraldii</i>
Leaf	pinnate with 7-11 leaflets, 3-6 cm. long, leaflets 4-10 mm. broad, finely ciliate when young	partly entire and partly pinnatifid with 3-5 leaflets 4-6 cm. long, lateral leaflets 5-14 mm. broad, entire leaves 2-2.5 cm. wide, glabrous	always entire broad ovate 4-10 cm. long, and 3-6 cm. broad, glabrous
Branches	with terminal bud	with or without terminal bud	without terminal bud
Panicles	4-7 cm. long, usually several pairs along the branches, sessile	to 11 cm. long, usually one pair at end of branches, sessile	to 15 cm. long, usually one pair at end of branches, peduncled
Corolla	white, usually tinged pale lilac, tube 5-6 mm. long, limb about 7 mm. across, lobes oval-ovate, not cucullate	whitish or bluish lilac, fading to whitish, tube about 8 mm. long, limb about 1 cm. across, lobes oval, slightly cucullate	lilac or purple lilac, tube 15-18 mm. long, limb about 1.5 cm. across, lobes oblong, strongly cucullate
Anthers	slightly exerted	anthers just reaching the mouth	anthers about 1.5 mm. below the mouth

This hybrid was raised in 1929 from seed collected in 1929 from *S. pinnatifolia* Hemsl. the flowers of which were apparently pollinated by a plant of *S. oblata* var. *Giraldii* (Lemoine) Rehd. not very far from *S. pinnatifolia*. In the same year, Dr. K. Sax fertilized *S. pinnatifolia*

with pollen of *S. oblata* var. *Giraldii* and plants were raised from this pollination; these plants have not yet flowered, but in their vegetative characters agree with the plant described above. The pollen of *S. pinnatifolia* is defective, at least that of our plant, and self-pollinated flowers produce no seeds. The hybrid is clearly intermediate between these two species, readily distinguished from both species by the partly pinnatifid and partly entire leaves. In the partly entire and partly pinnatifid leaves the hybrid resembles *S. persica* L. var. *laciniata*, which can be distinguished by the broadly decurrent often obtusish lobes of the leaves and by the narrower and generally smaller entire leaves, by the smaller panicles usually in several to many pairs along the branches, the absence of the terminal leaf-bud, and by the anthers not reaching the mouth.

A. R.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

HYPODERMELLA HIRATSUKAE, A NEW SPECIES OF HYPODERMATACEAE FROM JAPAN¹

GRANT D. DARKER

With plate 154

FIVE SPECIES of Hypodermataceae have been reported on conifers in Japan by Shirai and Hara (1927). Only one species, *Lophodermium pinastri* (Schr. ex Fr.) Chev., was listed as occurring on pines. The present paper describes a new Japanese species of Hypodermataceae of unusual interest which was encountered during a hasty examination of the Hypodermataceae in the Mycological and Pathological Herbarium of the United States Department of Agriculture in Washington, D. C. Grateful acknowledgment is made to Dr. C. L. Shear and Mr. John A. Stevenson for the privileges extended to the writer.

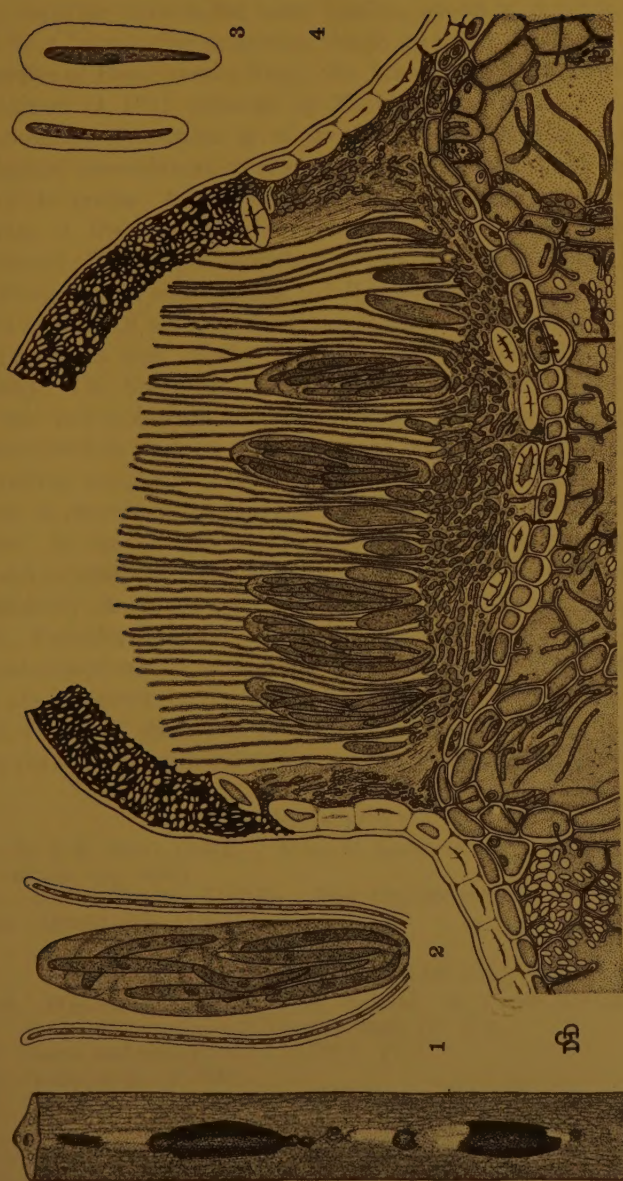
Hypodermella Hiratsukae, sp. nov.

Hysterotheciis in uno ordine epiphyllis oblongis ellipticisque atronitidis, $0.54-1.30 \times 0.26-0.34$ mm., longitudinali incisura aperientibus; hysterotheciis in transversali sectione in medio subcuticularibus sed ad marginem subepidermalibus, $0.16-0.22$ mm. profundis; basilari plectenchymate achroö $20-35 \mu$ crasso; tegente strato atri pseudoparenchymatis $28-34 \mu$ crasso; hymenio $100-110 \mu$ crasso. Ascis latis fusiformibusque octosporis $87-102 \times 18-24 \mu$. Paraphysibus $100-110 \times 1 \mu$ simplicibus filiformibus muco involutis. Ascosporis clavatis fusiformibusque ad basin attenuatis hyalinis $35-56 \times 3.5-5.0 \mu$, muco 8μ crasso involutis.

In foliis *Pini pumilae* Regel, in monte Kuro-dake, provinciae Ishikari Japoniae, mense Augusto, 1927, *Naohide Hiratsuka* legit.

Hysterothecia in a more or less continuous row, epiphyllous, oblong and elliptical, shining black, $0.54-1.30 \times 0.26-0.34$ mm., opening by a longitudinal fissure; hysterothecia in cross section subcuticular in the middle but subepidermal at margins, $0.16-0.22$ mm. deep (closed); basal layer colorless, plectenchymatous, $20-35 \mu$ thick; covering layer of dark pseudoparenchyma $28-34 \mu$ thick; hymenium $100-110 \mu$ thick. Asci broad, somewhat fusiform, truncate to rounded at maturity at tip, 8-spored, $87-102 \times 18-24 \mu$. Paraphyses $100-110 \times 1 \mu$, simple,

¹CONTRIBUTION FROM THE CRYPTOGAMIC LABORATORIES AND THE FARLOW HERBARIUM, HARVARD UNIVERSITY, No. 138.



HYPODERMELLA HIRATSUKAE Darker.

filiform, surrounded by a delicate gelatinous sheath. Ascospores clavate fusiform, tapering towards the base, hyaline, $36-56 \times 3.5-5.0 \mu$, surrounded by a conspicuous gelatinous sheath up to 8μ thick.

On needles of *Pinus pumila* Regel, Mt. Kuro-dake, Province Ishikari, Japan, August 12, 1927, collected by Naohide Hiratsuka.

Hypodermella Hiratsukae is of special interest because of certain morphological resemblances to *Hypodermella Laricis* v. Tub., the type species of the genus. As previously pointed out by the writer in 1932, the species of *Hypodermella* fall readily into four easily recognized groups named after the first described species in each as follows: (a) *H. Laricis* group, (b) *H. ampla* group, (c) *H. nervisequia* group, and (d) *H. sulcigena* group. Of nineteen species recognized in the genus, *H. Hiratsukae* approaches most closely *H. Laricis*, hitherto the only species in that group. The linear arrangement of the hysterothecia, the broad clavate asci and ascospores and the absence of a slit band along which the hysterothecium ruptures are common to both species. The position of the fruiting body of *H. Laricis* in the host tissue is difficult to determine even in microtome sections but is considered to be subcuticular by the writer. In the new species the hysterothecia are subcuticular in the centre and subepidermal at the margins as in *Lophodermium pinastri*. A prominently developed slit band, however, is characteristic of *L. pinastri*. Pycnidia with spores of the microconidial or spermatial type which are conspicuous and abundantly formed in the life cycle of *H. Laricis* are unknown in the case of *H. Hiratsukae* although in the material examined there are present certain small blister-like areas between the hysterothecia which may represent the remains of pycnidia.

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DESCRIPTION OF PLATE 154

- Fig. 1-4. *Hypodermella Hiratsukae*, sp. nov., on *Pinus pumila* Regel.
1. Portion of needle with hysterothecia ($\times 17$).
2. Ascus and paraphyses ($\times 500$).
3. Ascospores ($\times 500$).
4. Hysterothecium in cross-sectional view ($\times 270$ approx.).

FARLOW HERBARIUM, HARVARD UNIVERSITY,
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